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The use of functional traits as a tool in evaluating restorations of peatlands

rozprawa doktorska

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Streszczenie

Wstęp

Torfowiska niskie to ekosystemy bagienne odznaczające się stosunkowo stałym wysokim poziomem wód gruntowych zasobnych w sole mineralne, przesączających się przez złoże torfu lub występujących ponad jego powierzchnię (Rydin and Jeglum, 2006). Skład zbiorowisk roślinnych spotykanych na torfowiskach niskich zależy od współdziałania różnych czynników: pH (Sjörs and Gunnarsson, 2002, Wheeler and Proctor, 2000, Økland et al., 2001), dostępności substancji pokarmowych (Pauli et al., 2002, van der Hoek et al., 2004) i światła (Kotowski et al., 2001, Kotowski and van Diggelen, 2004) oraz poziomu wody (Kotowski et al., 2001, Mälson et al., 2008).

To współdziałanie czynników siedliskowych powoduje, że ekosystemy torfowisk niskich są wrażliwe na zmiany któregokolwiek z nich, a zaburzenie jednego czynnika często pociąga za sobą zmiany w pozostałych. Przykładem takiej zależności jest osuszanie torfowisk, prowadzące do obniżania się poziomu wody, co następnie prowadzi do napowietrzenia, do tej pory pozostającego w warunkach beztlenowych, torfu, uruchamiając jego mineralizację i uwalniając substancje odżywcze (Turner and Haygarth, 2001). To z kolei prowadzi do wzrostu produkcji pierwotnej (Joyce, 2001), pociągając za sobą zmniejszenie dostępności światła (Kotowski and van Diggelen, 2004), i w efekcie powodując ustępowanie typowych gatunków niskotorfowiskowych (Kotowski and van Diggelen, 2004, Sundberg, 2012, Vermeer and Berendse, 1983). Obniżenie się poziomu wód gruntowych powoduje też wzrost znaczenia wód opadowych, co prowadzi do zakwaszenia torfowiska (van Diggelen et al., 2006), czego następstwem jest zazwyczaj wzrost udziału torfowców (*Sphagnum spp.*), powodujących dalsze zakwaszanie poprzez mechanizm pozytywnego sprzężenia zwrotnego związany z wymianą jonów z otaczającymi je wodami (Rydin and Jeglum, 2006).

Degradacja i restytucja przyrodnicza

W XX wieku znaczne obszary torfowisk zostały osuszone w Europie w celu przekształcenia w obszary rolnicze, leśne lub na potrzeby wydobycia torfu (Vasander et al., 2003). W 1997 r. podawano, że 62% europejskich bagien (tj. żywych, akumulujących torf, torfowisk) zostało zniszczonych, a jedynie 5% było objętych ochroną (Joosten, 1997). Procesom tym stara się przeciwdziałać ochrona i restytucja przyrodnicza, a działań restytucyjnych potrzebują torfowiska niezależnie od ich objęcia ochroną obszarową.

Stowarzyszenie na rzecz Restytucji Przyrodniczej (Society for Ecological Restoration) definiuje restytucję przyrodniczą jako proces wspomagania regeneracji ekosystemu, który został zdegradowany, uszkodzony lub zniszczony (Society for Ecological Restoration International Science & Policy Working Group, 2004). Celem restytucji przyrodniczej torfowisk niskich jest odtworzenie zarówno warunków abiotycznych (hydrologii, dostępności światła i odpowiedniego poziomu żyzności) jak i biotycznych (skład gatunkowy). Z punktu

widzenia procesów kształtowania się zbiorowisk, restytucja przyrodnicza jest próbą zmiany działania filtów środowiskowych (biotycznych jak i abiotycznych), które w miejscu restytucji utrudniają rozwój zbiorowisk roślinnych podobnych do występujących w analogicznych ekosystemach niezaburzonych (zwanych dalej „ekosystemami referencyjnymi" lub „miejscami referencyjnymi"). Jeśli stopień degradacji torfowiska niskiego był stosunkowo niewielki, np. w przypadku umiarkowanego osuszenia dla gospodarki leśnej, najczęściej stosowaną metodą restytucji jest podniesienie poziomu wody poprzez zatamowanie rowów odwadniających i równocześnie usunięcie drzew w celu poprawienia warunków świetlnych (Haapalehto et al., 2011, Hedberg et al., 2012, Laine et al., 2011, Lanta et al., 2006, Mälson et al., 2008, Mälson et al., 2010). W przypadku silnie zdegradowanych obszarów, na których powierzchniowa warstwa torfu uległa mineralizacji, prowadząc do akumulacji pierwiastków biogennych, coraz częściej stosowaną metodą restytucji jest usunięcie powierzchniowej warstwy gleby (murszu). Zabieg ten pozwala na równoczesne zwiększenie uwilgotnienia, usunięcie niechcianego banku nasion, zwiększenie dostępności światła oraz usunięcie substancji odżywczych i w konsekwencji obniżenie żyzności (Klimkowska et al., 2010a, Patzelt et al., 2001, Rasran et al., 2007, Tallowin and Smith, 2001). Jeśli na obszarze restytucji przyrodniczej nie zachowały się pierwotne zespoły roślin, a ograniczenia w rozprzestrzenianiu się gatunków utrudniają naturalną rekolonizację obszaru restytucji, dla otworzenia docelowych zespołów roślinnych konieczna jest reintrodukcja gatunków. Najczęściej stosowanymi w tym celu metodami są: bezpośredni wysiew nasion gatunków docelowych (Fraser and Madson, 2008, Tallowin and Smith, 2001) oraz przenoszenie siana nasiennego zebranego na obszarach referencyjnych (Hölzel and Otte, 2003, Klimkowska et al., 2010a, Patzelt et al., 2001, Rasran et al., 2007).

W związku ze wspomnianą mnogością czynników wpływających na skład zbiorowisk roślinnych na torfowiskach niskich (m. in. warunki hydrologiczne, dostępność światła, pH, żyzność), restytucja przyrodnicza tych ekosystemów jest zadaniem niełatwym, a obszary poddane restytucji rzadko w pełni upodabniają się do referencyjnych (Moreno-Mateos et al., 2012). Względny sukces restytucji przyrodniczej był dotychczas przeważnie oceniany za pomocą takich wskaźników, jak liczba gatunków docelowych, które się osiedliły, lub wskaźniki łączące informacje o obecności gatunków i o ich liczebności (Shannon, 1948, Simpson, 1949), a także metod ordynacyjnych opartych o informacje o występowaniu gatunków i ich liczebnościach. Takie metody mogą dać odpowiedź na pytanie w jakim stopniu skład gatunkowy zbiorowisk na obszarze restytucji jest podobny do tego na obszarze referencyjnym, nie są jednak w stanie wyjaśnić ekologicznych przyczyn obserwowanych podobieństw lub różnic pomiędzy tymi zbiorowiskami. Co więcej, ocena dokonana na podstawie przynależności gatunkowej zatraca swoją użyteczność poza geograficznym obszarem występowania badanych gatunków.

Nowe możliwości analizy różnorodności funkcjonalnej

Analiza oparta na cechach funkcjonalnych gatunków pozwala przezwyciężyć ograniczenia analizy opartej wyłącznie na składzie gatunkowym zbiorowisk. W ekologii funkcjonalnej, wskaźniki różnorodności funkcjonalnej zostały zaproponowane jako miara uwzględniająca funkcje poszczególnych gatunków w ekosystemie (Diaz and Cabido, 2001,

Díaz et al., 2007, Garnier et al., 2004, Garnier et al., 2007, Laliberté and Legendre, 2010, Mason et al., 2005, Villéger et al., 2008). Pomimo, że różnorodność funkcjonalna wydaje się pomocna w ocenie na ile ekosystem będący efektem restytucji różni się pod względem funkcjonalnym od ekosystemu referencyjnego, czy też w identyfikacji filtrów ekologicznych, które wpłynęły na efekt restytucji, wykorzystujące ją metody nie były dotychczas stosowane do opisywania restytucji przyrodniczej. Zakładając, że skład gatunkowy zbiorowisk roślinnych występujących na torfowiskach niskich jest efektem działania różnych filtrów środowiskowych, w szczególności anoksji glebowej (siny filtr abiotyczny) (Kotowski et al., 2010) i konkurencji o światło (filtr biotyczny) (Kotowski and van Diggelen, 2004), analiza rozkładu cech funkcjonalnych gatunków powiązanych z ich reakcją na działanie tych filtrów może być podstawą oceny podobieństwa odtwarzanego ekosystemu do ekosystemu referencyjnego oraz może wskazać w jaki sposób konkretne cechy gatunków były promowane w procesie restytucji. Użycie metod ekologii funkcjonalnej może też wskazać, które gatunki docelowe mają największe prawdopodobieństwo osiedlenia się, a także może pomóc w doborze metod restytucji zwiększających prawdopodobieństwo odtworzenia populacji gatunków o określonych cechach funkcjonalnych.

W swoich badaniach skoncentrowałem się na możliwościach wykorzystania różnorodności funkcjonalnej w badaniach nad restytucją przyrodniczą torfowisk niskich. Możliwości te dotyczą przede wszystkim dostarczania informacji o tym, jak restytucja przyrodnicza modyfikuje filtry środowiskowe, umożliwiając skuteczne osiedlenie się tylko gatunkom o specyficznych wartościach cech funkcjonalnych, a także o tym, na ile zbiorowisko roślinne kształtujące się na obszarze restytucji różni się pod względem rozkładu cech funkcjonalnych od zbiorowiska referencyjnego. Porównanie tych dwóch zbiorowisk pod względem rozkładu cech funkcjonalnych powinno wskazać na różnice filtrów środowiskowych, a tym samym pokazać jakie czynniki utrudniają osiągnięcie stanu referencyjnego w odtwarzanym ekosystemie.

Opracowano wiele wskaźników różnorodności funkcjonalnej. W swoich badaniach ograniczyłem się do czterech, które ze względu na swoją konstrukcję powinny umożliwiać objaśnianie filtrów środowiskowych działających w trakcie restytucji. Trzy z pośród tych wskaźników zostały zaproponowane przez Masona i in. (2005) (bogactwo funkcjonalne - *functional richness*, równomierność funkcjonalna - *functional evenness* oraz rozbieżność funkcjonalna- *functional divergence*), a ostatni, rozproszenie funkcjonalne (*functional dispersion*), przez Laliberté and Legendre (2010). Oprócz tych wskaźników, analizowałem także średnie wartości cech funkcjonalnych dla zbiorowisk ważone ilościowością gatunków, a także obfitość gatunków w grupach funkcjonalnych.

Trzy wskaźniki zaproponowane przez Masona i in. (2005), a następnie opracowane jako elementy analizy wielocechowej przez Villégera i in. (2008) (bogactwo funkcjonalne, równomierność funkcjonalna oraz rozbieżność funkcjonalna) mierzą odpowiednio: objętość bryły w wielowymiarowej przestrzeni tworzonej przez wartości cech poszczególnych gatunków w zbiorowisku, równomierność rozkładu biomasy w obrębie tej bryły oraz rozkład ilościowości poszczególnych gatunków w obrębie owej bryły. Opisują one różne aspekty różnorodności funkcjonalnej. Laliberté and Legendre stwierdzili jednak, że przywiązanie bogactwa funkcjonalnego do wypukłej bryły wielowymiarowej czyni ten wskaźnik wrażliwym na ekstremalne wartości poszczególnych cech oraz zbyt mało związanym z różnicami ilościowości poszczególnych gatunków. Z kolei równomierność i rozbieżność funkcjonalna

biorą pod uwagę ilościowość gatunków ale nie zawierają informacji o ich położeniu w obrębie wielowymiarowej bryły tworzonej przez ich cechy. Autorzy ci zaproponowali więc nowy wskaźnik – rozproszenie funkcjonalne, zdefiniowane jako średnia odległość wszystkich gatunków od centroidu wszystkich gatunków w przestrzeni cech funkcjonalnych (Laliberté and Legendre, 2010).

Opis badań przeprowadzonych w pracy doktorskiej

Na niniejszą rozprawę doktorską składają się cztery odrębne publikacje, podejmujące różne aspekty restytucji przyrodniczej torfowisk niskich.

Publikacja nr 1 jest meta-analizą skuteczności różnych metod introdukcji gatunków w projektach restytucji przyrodniczej torfowisk niskich i łąk półnaturalnych. W tym celu została przeprowadzona szczegółowa kwerenda literatury światowej w poszukiwaniu wyników badań nad projektami restytucji, w których stosowano introdukcję gatunków. Używane metody zostały opisane jakościowo i ilościowo, a sukces każdej z nich został oszacowany na podstawie informacji o tym jak wiele spośród gatunków docelowych osiedliło się na obszarze restytucji. W analizie uwzględniono także dodatkowe informacje przekazywane przez autorów na temat wyników restytucji, jeśli tylko były one dostępne.

Meta-analiza metod introdukcji gatunków w restytucji przyrodniczej zdegradowanych torfowisk niskich i łąk półnaturalnych wskazała na transfer siana nasiennego z obszarów zbliżonych do ekosystemów referencyjnych jako na metodę pozwalającą skutecznie odtwarzać całe zbiorowiska roślinne. Nie oznacza to jednak że metoda ta jest zawsze lepsza od innych, ponieważ skuteczność każdej z nich zależy od czynników zewnętrznych. Transfer siana, czy wysiew gatunków nie są na przykład odpowiednie do wprowadzania gatunków rzadkich lub o niskiej zdolności kiełkowania, czy słabej przeżywalności siewek. Badania przeprowadzone w trakcie projektu restytucji przyrodniczej na Bagnie Całowanie pokazały ponadto, że samo przeniesienie siana, bez wprowadzania zaburzeń gleby (takich jak usuwanie jej powierzchniowej warstwy), ma bardzo mały wpływ na skład gatunkowy zbiorowisk roślinnych, a z kolei metodę usuwania wierzchniej warstwy gleby trudno rekomendować w przypadku umiarkowanie zniszczonych systemów, takich jak obiekty badawcze w Szwecji.

W następnej kolejności opisane są wyniki szwedzkiego projektu restytucji trzech torfowisk niskich osuszonych w latach 50-tych XX wieku na potrzeby gospodarki leśnej. Obiekty te zostały w 2002 r. poddane zabiegom restytucji przyrodniczej, polegającym na usunięciu posadzonych wcześniej drzew oraz zablokowaniu rowów odwadniających. Wpływ tych działań na zbiorowiska roślinne poddano analizie zarówno klasycznymi metodami, koncentrując się na składzie gatunkowym, jak i metodami ekologii funkcjonalnej. Zmiany zbiorowisk roślinnych na trzech szwedzkich obiektach były monitorowane w okresie 2002-2010 i porównane z ekosystemem referencyjnym – niezmeliorowanym torfowiskiem monitorowanym w latach 1978-1979. Publikacja nr 2 przedstawia wyniki restytucji w ujęciu funkcjonalnych grup gatunków, a publikacja nr 3 – w oparciu o analizę wskaźników różnorodności funkcjonalnej.

Zastosowanie analizy wykorzystującej podział gatunków na grupy funkcjonalne (publikacja nr 2) pokazało wyraźnie, że zarówno zwiększenie uwilgotnienia, jak i usunięcie drzew, doprowadziły do zwiększenia się pokrycia torfowców, innych mchów bagiennych oraz turzyc. Samo usunięcie drzew doprowadziło do wzrostu pokrycia traw, gatunków bagiennych roślin naczyniowych oraz siewek drzew. Każda z tych metod restytucji doprowadziła do wzrostu bogactwa gatunkowego roślin naczyniowych i mszaków na obszarze restytucji, ale najwyższe bogactwo gatunkowe było wynikiem ich łącznego zastosowania. Mimo to, wyspecjalizowane gatunki zasobnych w sole mineralne torfowisk niskich, które były gatunkami docelowymi restytucji, nie osiedliły się, najprawdopodobniej ze względu na ograniczenia dyspersji. Stosując metody analizy funkcjonalnej (publikacja nr 3), mogliśmy wykazać, że restytuowane ekosystemy miały wyższe bogactwo funkcjonalne, większe rozproszenie funkcjonalne i większą średnią wysokość gatunków roślin w porównaniu z obszarami referencyjnymi, co wskazuje na mniej intensywne filtrowanie puli gatunków w odtwarzanym zbiorowisku. Samo usuwanie drzew zwiększyło bogactwo funkcjonalne i rozproszenie funkcjonalne, co także wskazuje na zmniejszenie filtrowania środowiskowego po usunięciu zacienienia.

Ze szwedzkimi obiektami badawczymi kontrastował projekt restytucji przyrodniczej torfowisk niskich na położonym 30 km na południowy-wschód od Warszawy Bagnie Całowanie, które zostało w przeszłości osuszone na potrzeby rolnictwa (publikacja nr 4). W 2008 roku, w ramach projektu restytucji usunięto tu zdegradowaną warstwę gleby (murszu) i wprowadzono gatunki docelowe metodą transferu siana nasiennego ze zbiorowisk referencyjnych. Obszar usuwania murszu został podzielony na pasy, na których naprzemiennie zastosowano, bądź nie zastosowano przenoszenie siana nasiennego, co umożliwiło ocenę efektów usunięcia wierzchniej warstwy gleby zarówno w wariancie z transferem siana nasiennego i bez tego zabiegu. Jako kontrolę zastosowano poletka na zdegradowanym torfowisku, z którego nie usunięto warstwy murszu, gdzie również rozrzucono siano nasienne. Rozwój zbiorowisk w każdym z wyżej wymienionych wariantów (usuwanie zdegradowanej gleby z transferem siana nasiennego i bez oraz kontrola z transferem siana i bez), a także na obszarze referencyjnym, z którego pozyskano siano nasienne, monitorowano następnie na stałych powierzchniach badawczych. W obrębie obszarów usuwania murszu poletka badawcze były rozmieszczone w taki sposób, aby reprezentowały pełen gradient zmienności wysokości powierzchni tego obszaru względem poziomu wody, tak aby zmienna ta mogła być wykorzystana jako czynnik wyjaśniający rozwój zbiorowisk roślinnych. Wyniki restytucji na Bagnie Całowanie były analizowane zarówno tradycyjną metodą, opartą na składzie gatunkowym, jak i w oparciu o różnorodność funkcjonalną.

Wielocechowa analiza RDA danych zebranych na Bagnie Całowanie (publikacja nr 4) pokazała, że zbiorowiska roślinne obszarów objętych restytucją oraz referencyjnych wyodrębniają się od kontrolnych (zdegradowanych) wzdłuż pierwszej osi ordynacji, którą można interpretować jako gradient wilgotności. Transfer siana miał stosunkowo niewielki wpływ na kształtowanie się zbiorowisk w porównaniu z usuwaniem murszu. Metodami klasycznej analizy udało się także zaobserwować zależność pomiędzy poziomem wody gruntowej, a obfitością występowania gatunków. Używając metod ekologii funkcjonalnej mogliśmy wykryć, że poziom zwierciadła wody działa jako silny filtr środowiskowy wyrażający się istotnym spadkiem bogactwa funkcjonalnego i rozproszenia funkcjonalnego wraz ze wzrostem średniego poziomu wody gruntowej. W warunkach wysokiego poziomu wody

przez ten filtr siedliskowy przedostają się gatunki, posiadające zdolność do efektywnego rozprzestrzeniania wegetatywnego, przystosowania do anoksji (wyrażone wysoką liczbą wskaźnikową Ellenberga dla wilgotności), hydrochoryczny sposób rozprzestrzeniania nasion, niski stosunek powierzchni liści do masy (SLA) i nie rozprzestrzeniające się za pomocą autochorii. Ponadto, wykazaliśmy, że obszary restytucji różnią się od obszarów referencyjnych mniejszym udziałem gatunków autochorycznych, prawdopodobnie w związku ze słabym przenoszeniem takich gatunków z sianem, co potwierdziła analiza funkcjonalna składu gatunkowego diaspor znajdujących się w wykorzystywanym sianie nasiennym. Ważną grupą, na którą zjawisko to oddziaływało niekorzystnie były turzyce, będące równocześnie gatunkami docelowymi restytucji.

Wnioski

Moje badania były prowadzone w dwóch krajach, w miejscach odległych od siebie nawet o 960 km w linii prostej. Obiekty badawcze różniły się budową geologiczną, historią użytkowania, stopniem degradacji, a także warunkami klimatycznymi takimi jak długość i początek okresu wegetacyjnego. W związku z powyższym, lokalne pule gatunków roślin były na tych obszarach różne. Podczas gdy szwedzkie obiekty badań charakteryzowały się znacznym udziałem mszaków, włączając w to obfite występowanie torfowców na dwóch spośród trzech obiektów, torfowisko Całowanie było zdominowane przez trawy, turzyce i byliny dwuliścienne zróżnicowane w gradiencie wilgotności od roślin obszarów silnie przesuszonych na poletkach kontrolnych do gatunków mokrych łąk i torfowisk odnajdowanych na obszarach poddanych restytucji. W najniżej położonych miejscach pojawiały się nawet gatunki charakterystyczne dla zbiorników wodnych.

Znaczne różnice w składzie gatunkowym pomiędzy badanymi obszarami mogą utrudniać generalizację wniosków dotyczących tego jakie gatunki mają szanse skorzystania z konkretnych działań restytucji. Stosując metody ekologii funkcjonalnej zmieniamy pytanie o to, które gatunki skorzystają na restytucji na pytanie o cechy gatunków i ich kompozycję w zbiorowisku, które będą faworyzowane przez konkretne działania restytucji. Ta zmiana podejścia umożliwia wysnuwanie wniosków niezależnych od lokalnych uwarunkowań i puli gatunków. Na podstawie informacji o tym jak działania restytucji zmieniają filtrowanie środowiskowe określonych cech funkcjonalnych gatunków, możemy lepiej przewidywać jak poszczególne gatunki zareagują na te działania, oczywiście pod warunkiem dostępności informacji o wartościach rozpatrywanych cech funkcjonalnych dla interesujących nas gatunków.

Analiza restytucji szwedzkich torfowisk oparta o grupy funkcjonalne pokazała, na ile poszczególne grupy gatunków skorzystały z wdrożenia jednego bądź obydwu działań restytucji, czyli podniesienia uwilgotnienia i usunięcia drzew. Przekonaliśmy się także o pozytywnym wpływie restytucji na bogactwo gatunkowe. Analiza ta nie pozwoliła nam jednak wnioskować o ekologicznych mechanizmach stojących za tymi wynikami. Dopiero analiza cech funkcjonalnych wskazała, że usunięcie drzew złagodziło filtrowanie środowiskowe na obszarze restytucji. To słabsze filtrowanie umożliwiło gatunkom, których kombinacja cech funkcjonalnych była do tej pory niekorzystna w lokalnych warunkach

siedliskowych, na wzrost i rozwój po restytucji. Zwiększenie uwilgotnienia może wpływać na produktywność w dwojaki sposób: poprzez rozwój anoksji może ją zmniejszać ale równocześnie produkcja pierwotna może wzrastać na nawodnionych torfowiskach, gdy z częściowo zmineralizowanego torfu uwalniają się nieorganiczne związki fosforu i azotu. Większa średnia wysokość roślin na obszarze objętym restytucją w porównaniu do obszaru referencyjnego może wskazywać, że te drugi mechanizm przeważał. Podobnie, oparta na cechach funkcjonalnych analiza wyników projektu restytucji na Bagnie Całowanie naświetliła ekologiczne przyczyny różnic w składzie gatunkowym. Badania prowadzone przeze mnie w Polsce i w Szwecji są przykładem wykorzystania analizy funkcjonalnych cech gatunków roślin do oceny efektów restytucji przyrodniczej. Nie mogą one całkowicie zastąpić klasycznych metod badawczych opartych o skład gatunkowy zbiorowisk, są jednak ich doskonałym uzupełnieniem, wskazującym ekologiczne przyczyny sukcesu lub porażki konkretnych gatunków w trakcie restytucji. Połączenie podejścia klasycznego, opierającego się na ilościowości gatunków, z analizą cech funkcjonalnych umożliwia prowadzenie badań nad efektami restytucji, których wyniki z jednej strony odnoszą się do konkretnych gatunków będących przedmiotem naszych działań, a z drugiej strony mogą być zastosowane poza obszarem ich występowania, wnosząc nową jakość do nauki o restytucji przyrodniczej.

Publikacje składające się na tą pracę

Poniżej przedstawiono listę publikacji zawartych w mojej rozprawie doktorskiej. Deklaracje współautorów o ich wkładzie w poszczególne prace zamieszczono w załącznikach.

1:

Hedberg, P. & Kotowski, W. 2010. New nature by sowing? The current state of species introduction in grassland restoration, and the road ahead. *Journal for Nature Conservation,* 18**,** 304–308.

Impact factor 2010: 1.545

Mój udział w tej pracy szacuję na 80%. Polegał on na poszukiwaniu i analizie danych literaturowych, napisaniu artykułu oraz odpowiadaniu na uwagi recenzentów.

2:

Hedberg, P., Kotowski, W., Saetre, P., Mälson, K., Rydin, H. & Sundberg, S. 2012. Vegetation recovery after multiple-site experimental fen restorations. *Biological Conservation,* 147**,** 60-67.

Impact factor 2012: 3.794

Mój udział w tej pracy szacuję na 55%. Polegał on na monitorowaniu składu gatunkowego zbiorowisk w 2010r., pomiarach wysokości na powierzchniach badawczych, analizie wyników, napisaniu artykułu i odpowiadaniu na uwagi recenzentów.

3:

Hedberg, P., Saetre, P., Sundberg, S., Rydin, H. & Kotowski, W. 2013. A functional trait approach to fen restoration analysis. *Applied Vegetation Science,* 16**,** 658-666.

Impact factor 2012: 2.263

Mój udział w tej pracy szacuję na 65%. Polegał on na monitorowaniu składu gatunkowego zbiorowisk w 2010r., zebraniu informacji o cechach funkcjonalnych gatunków, analizach statystycznych, napisaniu artykułu i odpowiadaniu na uwagi recenzentów.

4:

Hedberg, P., Kozub, Ł. & Kotowski, W. 2013. Functional diversity analysis helps to identify filters affecting community assembly after fen restoration by top-soil removal and hay-transfer. *Journal for Nature Conservation*. DOI: 10.1016/j.jnc.2013.08.004 IN PRESS

Impact factor 2012: 1.535

Mój udział w tej pracy szacuję na 65%. Polegał on na założeniu eksperymentu terenowego, przeprowadzeniu monitoringu, analiz statystycznych, napisaniu artykułu oraz odpowiedziach na uwagi recenzentów.

Summary

Introduction

Fens are minerotrophic peatlands with the water table located very close to the ground level. The water flows through the peatland by internal seepage and occasional regions of surface overflow (Rydin and Jeglum, 2006). The composition of plant communities found in fens depends on a complex interplay of pH (Sjörs and Gunnarsson, 2002, Wheeler and Proctor, 2000, Økland et al., 2001), nutrient availability (Pauli et al., 2002, van der Hoek et al., 2004), light availability (Kotowski et al., 2001, Kotowski and van Diggelen, 2004) and water table depth (Kotowski et al., 2001, Mälson et al., 2008).

This interplay makes fen ecosystems vulnerable to changes in any of the above mentioned factors, and often a modification of one variable alters another variable. An example of this is drainage of fens, which lowers the water-table, which in turn aerates the previously anoxic peat, resulting in mineralization of the peat, with release of nutrients (Turner and Haygarth, 2001). This causes increased primary productivity (Joyce, 2001), which in turn lowers the light availability (Kotowski and van Diggelen, 2004), which has a detrimental effect on characteristic fen species (Kotowski and van Diggelen, 2004, Sundberg, 2012, Vermeer and Berendse, 1983). The lowered water-table increases the influence of rain-water. This results in acidification (van Diggelen et al., 2006), usually followed by an increase in peat mosses (*Sphagnum* spp.) which causes a positive feedback of further acidification, due to ion-exchange between *Sphagnum* spp. and its local surrounding (Rydin and Jeglum, 2006).

Degradation and restoration

During the 20th-century large areas of peatlands in Europe were drained for agricultural production, forestry purposes or peat extraction (Vasander et al., 2003). In 1997 it was reported that 62 % of Europe's mires (peat accumulating peatlands) have been lost, and only 5 % is protected (Joosten, 1997). Attempts to counteract this development include conservation and restoration, although even the protected areas include peatlands that are in strong need of restoration (Sundberg, 2006).

Ecological restoration as defined by the Society for Ecological Restoration is the process of assisting the recovery of an ecosystem that has been degraded damaged or destroyed (Society for Ecological Restoration International Science & Policy Working Group, 2004). Ecological restoration of fens aims at restoring both the abiotic factors (hydrology, light-availability and nutrient-concentration) and the biotic factors (species assemblage). Expressed in terms of community assembly rules, the restoration aims to alter the environmental filters (abiotic and biotic) that limits the restoration site from developing species communities similar to those found in analogous undisturbed ecosystems (further on called 'reference ecosystems' or 'reference sites'). In moderately degraded fens, i.e. cases of moderate drainage for forestry purposes, a common restoration method is the combination

of rewetting by blocking drainage ditches and tree-cutting to restore the light-conditions (Haapalehto et al., 2011, Hedberg et al., 2012, Laine et al., 2011, Lanta et al., 2006, Mälson et al., 2008, Mälson et al., 2010). In heavily degraded fens, were the peat has mineralized, resulting in excess nutrient-concentration, an increasingly applied restoration method is top-soil removal. This restoration method has the capacity to increase the ground-water level, remove the unwanted seed-bank, increase light-conditions and remove excess nutrients (Klimkowska et al., 2010, Patzelt et al., 2001, Rasran et al., 2007, Tallowin and Smith, 2001). In cases where the original species community has vanished, and dispersal limitation makes natural colonization into the restoration-site improbable, species have to be introduced in order to restore the species-community. Among methods used to introduce communities of species, direct seeding (Fraser and Madson, 2008, Tallowin and Smith, 2001) and hay-transfer from reference-meadows (Hölzel and Otte, 2003, Klimkowska et al., 2010, Patzelt et al., 2001, Rasran et al., 2007) are commonly used.

Due to the mentioned multitude of factors influencing the species community in a fen (e.g. hydrology, light, pH and nutrient concentration), ecological restoration is difficult, and restoration sites rarely reach the conditions of the reference sites (Moreno-Mateos et al., 2012). The relative success of ecological restoration has mostly been measured in terms of numbers of target species present, indices that combine species identity and relative abundance of each species (Shannon, 1948, Simpson, 1949) or ordination methods based on species identity and abundance. These methods can provide information regarding how the species composition at the restoration site compares to that of the reference site, but provide no ecological explanation for any similarity or difference that is detected. Secondly, an evaluation based on species identities loses its usefulness outside the geographical distribution-range of the studied species.

The advent of functional diversity

A solution to the limits of the species-identity focused analysis is to turn the attention to the functional characteristics the species possess. In functional ecology functional diversity measures have been put forward as a measure that takes into account the functions of species (Diaz and Cabido, 2001, Díaz et al., 2007, Garnier et al., 2004, Garnier et al., 2007, Laliberté and Legendre, 2010, Mason et al., 2005, Villéger et al., 2008). Although functional diversity appears to have the potential to highlight if and how a restoration site differs in functional composition from the reference site, as well as describing the environmental filters that influence the outcome of the restoration project, the methods have not been applied to restoration ecology. Considering that species composition in fens is influenced by several ecological filters, i.e. anoxia (a strong abiotic filter) (Kotowski et al., 2010) and competition for light (a biotic filter) (Kotowski and van Diggelen, 2004), the application of a functional analysis for traits corresponding to these filters may be useful for ecologists when analysing if the species community in the restoration site is functionally similar to the species community in the reference site, and how specific traits are filtered by the restoration measures. With this tool ecologists would have the potential to, based on functional analyses of similar restoration projects, determine which target species are likely

to establish, and adapt restoration measures in order to increase the chance of successful establishment of species carrying certain traits.

My research focused on the potential value of a functional diversity analysis in the analysis of fen restoration. The value lies in the potential in obtaining information on how restoration actions modify the environmental filters that only species with certain trait-values can pass, and how the species community in the restoration site differs in functional composition from the species community in the reference site. A difference in the functional composition between the species communities should indicate a difference in the environmental filters, and thereby pinpoint factors that constrain the restoration site from reaching the state of the reference-site.

A variety of functional diversity indices exists today. I have limited my research to 4 indices that, based on their structure, should have the potential to provide information on environmental filters in fen restoration. These four indices are the three indices presented by Mason et al. (2005) (functional richness, functional evenness and functional divergence), as well as functional dispersion (Laliberté and Legendre, 2010). Apart from these, the Community Weighted Means of the functional traits are analysed, as well as the functional group abundance.

The three indices put forward by Mason et al. (2005) and placed into a multivariate context by Villéger et al. (2008) (functional richness, functional evenness and functional divergence) measure the size of the filled niche space, the evenness of biomass distribution within a niche space and the abundance distribution within a niche space respectively. These three indices all describe different facets of functional diversity. However, Laliberté and Legendre pointed out that the connection to the convex-hull makes functional richness sensitive to outliers, and that functional richness does not take into consideration the relative abundance of species. Functional evenness and functional divergence on the other hand include the relative abundance of species, but lack information on the distribution of species in the trait space. Their solution to this was the index functional dispersion, which is a measure of the dispersion of trait values in a trait space, defined as the average distance of all species to the centroid of all species in a trait space (Laliberté and Legendre, 2010).

Description of the research conducted for this thesis

This thesis consists of four individual publications, in which various aspects of the restoration of fens have been explored.

The first publication is a meta-analysis of the diversity and relative success of species introduction methods in restoration of fens and semi natural grasslands, carried out by conducting an extensive search for studies that used introduction of species as a part of ecological restoration. The introduction-methods used were described and quantified, and the success of each method was evaluated based on how many of the introduced species that established in the restoration site. When available, the authors written comments about their view of the restoration were included as a variable in the evaluation.

The analysis showed that in many cases species introduction through the transfer of hay from donor-meadows is a successful method for restoring species communities. This is not to say that the method is superior to any other species introduction method, since external factors may considerably change which method is most suitable. An example of this is that direct seeding or hay spread may not be recommended if the species are rare, have low germination rate or low seedling survival. Further the application of hay-transfer in the restoration of Całowanie fen showed that hay transfer without ground-disturbance (such as top-soil removal) has very little impact on the species community, and if the degradation is moderate, as in the Swedish sites, then complete removal of the vegetation may not be recommended.

Following this a Swedish fen restoration project covering three fens that were drained for forestry purposes in the 1950s and restored in 2002 by cutting planted trees and blocking drainage ditches was analysed both through a functional group-focused analysis (publication 2) and through a functional trait diversity analysis (publication 3). The vegetation changes in the three Swedish restoration sites were monitored between 2002-2010 and compared to a reference-site that was monitored between 1978-1979 prior to it was drained. The application of a functional group-focused analysis in the Swedish fen restoration projects (publication 2) clearly showed that both rewetting and tree cutting increased the cover of Sphagnum, wetland bryophytes and sedges. Tree cutting increased the cover of grasses, wetland vascular plants and juvenile trees. Both treatments resulted in an increase in species richness, and the combination of the two treatments resulted in the highest species-richness. However, the rich-fen specialists that were the target of the restoration did not recover, most likely due to dispersal limitation. By applying a functional trait analysis (publication 3) we could detect that the restoration sites had a higher functional richness, a higher functional dispersion and a higher canopy height than the reference-sites, which indicates a too relaxed filter. Tree cutting resulted in an increase in functional richness and functional dispersion, which indicates a lowered habitat filter after the removal of the shading canopy.

As a contrast to the Swedish restoration project, I analysed the outcome of an ecological restoration of Całowanie fen located 30 km south-east of Warsaw that previously had been drained for agricultural production (publication 4). Fen restoration in Całowanie was conducted in 2008 by removing the degraded top-soil, and introducing target species from donor meadows via hay-transfer. The top-soil removal site was divided up into belts, and hay was dispersed on every second belt, providing the possibility to analyse the effect of top-soil removal with and without hay-dispersal. As a control, hay from the donor meadows were also dispersed on control plots where no top-soil removal was conducted. I monitored permanent plots located in all treatment-types (top-soil removal with and without hay-transfer and control-plots with and without hay-transfer), as well as in donor meadows. Within the top-soil removal sites, plots were distributed in such a way that the gradient of relative water table depth was covered so that each plot's distance to the ground-water level could be included as an explanatory variable in the community analysis. The outcome of the restoration was analysed both through a classical species-identity focused analysis and through a functional trait analysis. A multivariate RDA analysis of the restoration in

Całowanie fen (publication 4) showed clearly that the top-soil removal site and the reference-site were separated from the control site along the first ordination axis, which followed a wetness gradient. Hay-dispersal had very little influence on the species community compared to the effect of top-soil removal. We could also through the classical analysis detect that characteristic species responded significantly in abundance to the ground-water level. By applying a functional trait analysis we could detect that the ground-water level imposes a strong habitat filter revealed by a significant decrease in functional richness and functional dispersion with increasing ground-water level. At high ground-water level this habitat filter selects for capacity for clonal lateral spread, high Ellenberg moisture values, capacity for hydrochorous dispersal and low specific leaf area and lack of capacity for autochorous dispersal. Further, we could detect that the restoration site differs in trait composition from the reference site by having a significantly lower proportion of species that disperse through autochory, which was probably caused already at the harvesting of the hay from the donor meadows, as indicated by the functional trait analysis of species present as seeds in the harvested hay. Among the species groups that are disfavoured by this are sedges, which were a target species group of the restoration.

Conclusions

My research has taken place in two countries in sites located up to 960 km from each other. The research sites differ in geological history, land-use history, degree of degradation, climatic conditions and length and start of vegetation season. As a consequence, there are also differences in species pools as well. Whereas the Swedish sites had a large bryophyte cover, including an abundance of *Sphagnum* species in two out of the three Swedish sites, the Całowanie fen was dominated by grasses, sedges and herbs spanning from species typical for heavily degraded fens that were found in the unrestored control sites, to species typical for wet meadows and fens found in restored sites. Limnic species could be found in the deepest parts of the restored sites.

Large differences in species-composition between geographic areas can cause considerable challenges in drawing site-independent conclusions regarding which species are likely to benefit from a specific restoration action. By applying a functional approach we switch the focus from which species will benefit from the restoration measures to which trait values and trait composition will species favoured by the restoration measures have. This switch of focus enables general site-independent conclusions to be drawn despite differences in species pools. Having data on how species possessing different trait-values are filtered by specific restoration actions, allows us to better predict how specific species are likely to respond to a specific restoration action, as long as trait-data for these species are available.

With the functional-group based analysis we could in the Swedish fen-restorations conclude that certain groups of species benefitted from one or both of the restoration actions - tree cutting and rewetting. We could also detect that the species richness was higher in the restored sites than in the reference sites. We could however not find any ecological explanation to why this was the case. With the functional-trait analysis

we could detect that the habitat filter in the restoration site was relaxed when the shading by canopy was removed. This weaker habitat filter allowed species of previously disfavoured trait-composition to flourish. Rewetting can influence productivity both by decreasing productivity by imposing anoxia, or increasing productivity by the release of phosphorous following rewetting of degraded peat. The higher canopy in the restoration site compared to the reference site indicates that productivity has increased due to release of phosphorous following rewetting of areas where previous drainage have caused the breakdown of peat, making nitrogen and phosphorous readily available. Similarly the functional-trait analysis of the restoration of Całowanie fen allowed us to get an ecological explanation to the results provided by the species based analysis. Together, the Swedish and Polish studies provide examples of how the functional trait analysis can be used in analysing the effect of restoration measures. Rather than being a replacement for the traditional analysis, it is a complement that provides an ecological explanation to why a specific species is likely to be favoured or disfavoured by a specific restoration action. With the combination of the traditional species-identity focused analysis and the functional-trait analysis we have the possibility to conduct restoration analyses that provides results that are both detailed in terms of effect on species in the study, but also relevant outside the distribution range of the present species, thus bringing added value to the science of ecological restoration.

Publications included in this thesis

Below follows a list of publications that are included in this thesis. Declarations of co-authors contributions are included as attachments.

1:

Hedberg, P. & Kotowski, W. 2010. New nature by sowing? The current state of species introduction in grassland restoration, and the road ahead. *Journal for Nature Conservation,* 18**,** 304–308.

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I assess my contribution of this publication to 80 %. My contribution included searching and analysing case studies, writing the manuscript, accounting for co-authors´ comments and accounting for reviewers' comments.

2:

Hedberg, P., Kotowski, W., Saetre, P., Mälson, K., Rydin, H. & Sundberg, S. 2012. Vegetation recovery after multiple-site experimental fen restorations. *Biological Conservation,* 147**,** 60-67.

Impact factor 2012: 3.794

I assess my contribution to this publication to 55 %. My contribution included monitoring, analysing data, writing manuscript, accounting for comments of co-authors´ comments and accounting for reviewers´ comments.

3:

Hedberg, P., Saetre, P., Sundberg, S., Rydin, H. & Kotowski, W. 2013. A functional trait approach to fen restoration analysis. *Applied Vegetation Science,* 16**,** 658-666.

Impact factor 2012: 2.263

I asses my contribution of this paper to 65 %. My contribution included monitoring, compiling trait-data, statistical analysis, writing the manuscript, accounting for co-authors´ comments and accounting for reviewers´ comments.

4:

Hedberg, P., Kozub, Ł. & Kotowski, W. 2013. Functional diversity analysis helps to identify filters affecting community assembly after fen restoration by top-soil removal and hay-transfer. *Journal for Nature Conservation*. DOI: 10.1016/j.jnc.2013.08.004 IN PRESS

Impact factor 2012: 1.535

I assess my contribution to this paper to 65 %. My contribution included dispersal of hay, depth measurements, monitoring, compiling trait data, statistical analysis, writing of manuscript, accounting for comment of co-authors´ and accounting for comments from reviewers.

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CHAPTER I

New nature by sowing? The current state of species introduction in grassland restoration, and the road ahead.

Petter Hedberg and Wiktor Kotowski

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New nature by sowing? The current state of species introduction in grassland restoration, and the road ahead

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ABSTRACT

Semi-natural grasslands are some of the most threatened habitats on the planet, due to the abandonment of small-scale farming and its replacement with intensive agriculture. The fragmented landscape of today has created dispersal limitation that makes improbable the natural dispersal of target species into the remaining patches of grassland. This paper reviews the current status of species introduction into semi-natural grasslands, and summarises the results of published literature in this field. Our review shows that restoration through species introduction is an effective method of establishing dispersal limited species. However, the field of species introduction in restoration ecology has yet to make use of the value that Functional Diversity can add to restoration. No single study in our search has followed up species introduction by measuring any of the currently available indices of functional diversity. This approach is necessary to gain knowledge on what traits are likely to be sorted out in species introduction cases in various environments.

Introduction

Until the end of the 19th century, farmlands in Europe consisted of vast areas of semi-natural grassland. In those times seed dispersal between populations occurred through the movement of hay, and through animal and wind dispersal. Farmers shared their equipment and unintentionally transferred plant seeds between different populations (Wallin et al. 2009). However, former semi-natural grassland has in our times been split up and exists in the form of islands of meadow in a fragmented landscape. During the Roman Empire, semi-natural grasslands expanded throughout Central Europe, and then declined sharply in the 19th and 20th centuries due to the abandonment of arable land and afforestation (Poschlod & WallisDeWries, 2002). An illustrative example of the sharp decline, is found in data from Sweden were the area of hay meadows has been reduced approximately from 1.2 million ha to 3000 ha, or to 0.25% of the original area (Wallin et al. 2009, Martinsson 1999). When grasslands are restored, in many cases species have to be introduced, since the formerly present species have disappeared from the vegetation and the seed bank (Walker et al. 2004).

Classical metapopulation theory states that dispersal between suitable patches drives a dynamic process of colonisation and extinction (Hanski 1999). In light of this, it is of great importance to preserve the still remaining patches of semi-natural grassland, as well as recreate degraded grasslands in order to increase habitats suitable for colonisation. In order for colonisation to occur, the diaspores have to be able to reach the available patch. That grassland communities experience dispersal limitation has been demonstrated in several studies (Verhagen et al. 2001; Tofts & Silvertown 2002; Franzén & Eriksson 2003; Kiehl & Pfadenhauer 2007; Klimkowska 2008; Stein et al. 2008). If a species cannot disperse effectively, it either has to germinate from the seed bank, or be dispersed artificially. Bossuyt and Honnay (2008) reviewed seed bank composition studies from 1990–2006, showing that grassland communities have very limited probability of establishing through germination from the seed bank. Heathlands are the only non-forest ecosystem, for which the study finds support of possible restoration through germination from the seed bank (Bossuyt & Honnay, 2008). Species from stable communities, such as permanent grasslands, are known not to invest in long lived seeds (Mitlacher et al. 2002), but rather in the clonal spread, and the competitive ability of seedlings (Bossuyt & Honnay, 2008). The result of this is the disappearance of the seeds from the seed bank soon after the species have disappeared from the vegetation.

A diversity of methods for introducing plants exists today, and the method chosen will have to be determined by the individual restoration practitioner based on the introduced plants characteristics for germination and establishment. Apart from this, the rarity of the species will affect which method is appropriate. Methods used for introducing a single species may differ

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substantially from the recommended method for introduction of a community of several species. In reality, the major constraint is often not necessarily the ability to determine the theoretically best method, but the cost to implement it. To our knowledge, no comprehensive review of the various methods used throughout the world for introducing species to grasslands has been made so far. This paper is an attempt to summarise experience of the various methods from different parts of the world, as well as their potential benefits and constraints.

Our review was conducted by using four sources of information.

1. ISI Web of Knowledge
2. JSTOR
3. Google
4. Personal knowledge of studies

The majority of studies were found as a result of the search at ISI Web of Knowledge. We used the max time-span, which at the time of our search was 1996–2009. Keywords used were "species introduction" and "species reintroduction". After refining the search 1882 studies were found to initially fit our criteria. Of these only the studies that described restoration cases were community introduction was carried out were included. The search on ISI was followed by searches using similar keywords on JSTOR and Google. One study known to us, but not found in the search due to very recent publication was included as well.

Based on the reviewed studies we distinguished the following methods of introduction:

(1) **direct seeding**, i.e. introducing species as seeds, collected in wild or obtained from cultivated plants, frequently in multi-species mixtures with proportions of species adjusted to their contribution in target communities;
(2) **diaspore transfer with substrate**, i.e. transferring vegetation with its substrate from the donor site to the restoration site; this method allows for including soil mycorrhizal fungi which are associated with the plant community (Cobbaert et al. 2004).
(3) **slot seeding** (strip-seeding), a modified version of direct seeding for a long time common in modern agriculture for sowing of grain; it is based on drilling the seeds into the soil with the help of a sowing machine, which reduces the amount of seed needed;
(4) **plug planting**, introduction of species through the use of plug plants (grown-up seedlings), is a method often used in forestry, and is recommended in grassland restoration when the species in question is rare (Morgan 1999), dispersal limited (Huddleston & Young 2004) or has a low establishments from seeds (Wallin et al. 2009);
(5) **hay spread**, i.e. transfer of seed-containing hay from reference communities, frequently used in European meadow restoration projects;
(6) **brush harvesting**, i.e. the transfer of seeds harvested with a brush harvester, which allows for drying, storage and separation of unwanted seeds before sowing.

Methods in practice

From 38 studies included in our review, 21 used direct sowing as the only or the main method of species introduction, hay spreading was used in 10 projects, whereas strip-seeding and plug planting is rarely used (four and five cases). Brush harvesting was only practiced in one study.

The popularity of direct seeding might be due to the ease of broadcasting seeds compared to the higher effort required for introducing plug plants or using strip-seeding. Direct seeding of plant species has also the advantage that the restoration practitioner knows what he/she is introducing. This might appear to be self evident information, but it is not. The main alternative, i.e. spreading hay, is often done without knowing the exact seed content of the hay.

Another problem encountered in community-level re-introductions is the amount of seeds, hay or plug-plants necessary when it comes to restoration of larger areas. This is usually solved by covering the area of restoration only partly by seeds or hay, assuming that the species will spread further on the site. In many cases strips of hay or seeds have been used, e.g. in mountainous meadows in White Carpathians ((Jongepierová et al. 2007) or floodplain meadows in the Rhine Valley (Hölzel & Otte 2003). However, the speed of species dispersal from the strips is still not clear and given the rate of dispersal of many meadow species rarely exceeding 10 m/year (van Dorp et al. 1996), one shouldn't expect fast spread of species, which are introduced into only small isolated patches.

Ecological effectiveness – do we know enough?

In order to evaluate whether a community introduction has been successful it is necessary to have a wide range of data. Information on which species were transferred, which species established and which species did not establish is fundamental for determining the effectiveness. Apart from this, some sort of abundance measure is helpful.

Each case-study in our review was given a grade (+) for successful introduction, (+/−) for limited success and (−) for failed introduction. Finally NA is given for studies where necessary information for evaluating the outcome is not available. 15 cases were regarded as (+), 9 cases were regarded as (+/−), 4 cases were regarded as (−) and 10 cases were regarded as (NA) (Table 1). The grades are based on our evaluation of the experiment in terms of established species out of all species introduced, and also the author's comments on the experiment.

The answer to the question whether the cases of species introduction in our review have been successful can be answered in two ways. Yes, if the definition of successful is that a large proportion of the introduced species get established, then many of the reviewed studies can be described as successful. It is clear though that the abundance of the established species vary greatly between cases, and that for many studies it is unclear how successful they have been due to the lack of information on introduced and/or established species.

Direct seeding did succeed in establishing dispersal-limited species in several cases, but there are notable exceptions such as the total failure of establishment of direct seeded species in the study by Tallowin and Smith (2001). Experiments in the UK indicate success of using direct seeding as well, especially in combination with mechanical disturbance (Walker et al. 2004). A multinational experiment in Sweden, the Netherlands, Spain, Germany and the UK showed an average establishment of 75% of the sown species, with a standard deviation of 21% (Lepš et al. 2007). Other studies have however raised concerns regarding the longer term survival of populations introduced by direct seeding (Wallin et al. 2009).

Introduction of species through hay spread is a method for introducing communities of grassland species that in several studies have been demonstrated to be successful. The method has been shown to have capacity to introduce some of the

Table 1
Studies containing reintroduction of species.

Authors	Location	ecotype	Method	Nr introduced	Nr established	Time (years)	Grade
Kiehl and Pfadenhauer 2007	DE	dry meadow	hay	80	71	9	+
Lepš et al. 2007	CZ	dry meadow	ds	16	13	7	+
Lepš et al. 2007	NL	dry meadow	ds	15	13	7	+
Lepš et al. 2007	GB	dry meadow	ds	15	15	7	+
Klimkowska et al. 2009	PL	wet meadow	hay	38	34	3	+
Foster et al. 2007	US	natural grassland	ds	32	23	5	+
Rasran et al. 2007	DE	fen	hay	41	14-33	4	+
Fenner and Spellerberg 1988	UK	dry meadow	ds	12	8	1	+
Fenner and Spellerberg 1988	UK	dry meadow	plug	12	9	1	+
Hoffman and Isselstein 2004	DE	dry meadow	ds	8	8	1	+
Hölzel and Otte 2003	DE	wet meadow	hay	≤124	102	4	+
Jongepierová et al. 2007*	CZ	dry meadow	ds	27	26	5	+
Patzelt et al. 2001	DE	wet meadow	hay	NA	57	6	+
Schmiede et al. 2009	DE	dry meadow	hay	NA	24-60	6	+
Stevenson et al. 1995	UK	dry meadow	ds	47	43	1	+
Lepš et al. 2007	SE	dry meadow	ds	15	9	7	+/−
Lepš et al. 2007	ES	dry meadow	ds	15	7	7	+/−
Camill et al. 2004	US	natural grassland	hay+ds	36	16	7	+/−
Foster and Lovett 2003	US	natural grassland	hay	17	9	6	+/−
Smith et al. 2000	UK	dry meadow	hay+ds	44	18	8	+/−
Brown and Bugg 2001	US	natural grassland	ds+plug	7	7	<1	+/−
Jones and Hayes 1999	UK	dry meadow	ds	5	5	1	+/−
Fraser and Madson 2008	US	wet meadow	ds	20	11	1	+/−
Tallowin and Smith 2001	UK	wet meadow	plug	14	8≤	1	+/−
Morgan 1999	AU	natural grassland	plug	48	19	>5	−
Tallowin and Smith 2001	UK	wet meadow	ds	28	0	4	−
Pywell et al. 2007**	UK	dry meadow	ss	18	4	4	−
Pywell et al. 2007**	UK	dry meadow	ss	18	1,87	4	−
Burke and Grime 1996	US	dry meadow	ds	54	NA	2	NA
Cobbaert et al. 2004	CA	fen	diasp+substr	NA	20≤	1	NA
Hopkins et al. 1999	UK	dry meadow	ss+ds	35-40	NA	2	NA
Hopkins et al. 1999	UK	dry meadow	plug	12	NA	2	NA
Holmes 2005	ZA	heathland	ds	NA	NA	3	NA
Martin and Wilsey 2006	US	natural grassland	ds	25	NA	<1	NA
Biondinini 2007	US	natural grassland	ds	50	NA	5	NA
Edwards et al. 2007	UK	dry meadow	hay	NA	NA	4	NA
Edwards et al. 2007	UK	dry meadow	brush	NA	NA	4	NA
Coulson et al. 2001	UK	dry meadow	ss	22	NA	3	NA

NA=Not available, ds=direct seeding, ss=strip seeding, hay=hay transfer, plug=plug plant, diasp+substr=diaspore+substrate transfer, brush=brush harvesting.

* Commercial grass mix excluded.
** Values are given as mean.

associated insect fauna as well (Kiehl & Wagner 2006). Studies from one site in Germany have shown the method's capacity in combination with topsoil removal to successfully establish 71 out of 80 species introduced with the hay (Kiehl & Pfadenhauer 2007). The study by Hölzel and Otte (2003) is another example of a successful hay transfer where several plant species established, including a number of threatened species. A Polish study showed that 34 out of 38 species found in the hay established (Klimkowska 2008) after topsoil removal. In order to correctly evaluate the effect of hay spread, the species present in the hay, as well as the species present in areas adjacent to the site of introduction, should be surveyed. This is unfortunately not always the case in the studies reviewed. Some of the reviewed studies assume that all species present in the donor site are transferred with the hay. It has however been demonstrated in other hay transfer studies that this is not the case (Kiehl & Pfadenhauer 2007).

Despite the success of strip seeding method in modern agriculture, its success in restoration of semi natural grassland is less obvious. The number of studies found using this method is too low to rule out the methods potential, but the two cases from (Pywell et al. 2007) do not give support to the method. In a comparative study of different sowing methods, slot seeding was shown to have only limited success compared to direct seeding combined with deturfing (Hopkins et al. 1999). The authors also point out that the use of rotovation in combination with slot seeding is likely to have increased the rate of nutrient mineralisation. For many target species this is counterproductive from a restoration point of view, since overload of nutrients have been shown to limit introduction success of target plants (Bakker & Berendse 1999).

The reports on using plug planting as an introduction show varied success. An evaluation by Morgan (1999) regarding whether this method had succeeded in restoring rare grassland species in Western Australia after eight years showed that none of the restoration sites had successfully produced second generation plants. The author concludes that most populations are already extinct, or are heading that way (Morgan 1999). The reason for this is unclear, and it is worth mentioning that the paper found no significant difference between the survival of rare plants when compared to more common plants. A Swedish study on the Baltic island of Gotland showed that plug plants performed worse than direct seeding for the species *Hypochoeris maculata* L. and *Succisa pratensis* Moench. on wooded hay meadows (Wallin et al. 2009). The authors found that roughly the same amounts of seeds were required for the plug plants compared to direct seeding. However, considering the higher long-term establishment of plug-plants they might be necessary despite the longer time and higher effort required to bring up seedlings when using plug-plants (Wallin et al. 2009).

The method is of use when the species is rare, and broadcasting of seeds or slot seeding would be a waste of seeds (Morgan, 1999).The method also has its advantage in introduction of late to mid successional species that are vulnerable to competition (Walker et al. 2004; Hopkins et al. 1999). This is further supported by a study showing that late successional woody plants have difficulties establishing when a perennial sward has been established. This is due to the limited bare ground that inhibits germination, and the competition for light, nutrient and water from the established vegetation (Smit & Olff 1998).

Only one study in our review used brush harvesting as introduction method and neither the number of species in the harvested seeds, nor how many out of these established is known. This gives us too little information for evaluating the method, but it's worth to notice that the numbers of species found in this study's plots was 119.

The studies in our review differ in the identity of the species that are introduced although some species are introduced in several studies. Apart from this, the management of the habitat prior to and during the experiments differ greatly between the studies. Considering the fact that a great number of species do not establish, it is clear that studies, which only report species above a certain limit of abundance might be missing a lot of potentially valuable information.

What can functional community ecology contribute?

Only knowing which species established, we will never be able to analyse why some species did not establish. If we are to gain a deeper understanding of why some species establish and some don't, we need to understand what functional traits the established community possess, and whether or not the traits of the species that did not establish are significantly different. Restoration ecology has traditionally focused on measuring diversity in terms of species richness solely, or through the use of indices related to the number of species and abundance of each species. Studies assessing how species richness and the functional components of diversity are related to ecosystem functioning, have generally found that the functional components of diversity are more consistently associated with the rates and magnitudes of ecosystem processes than is species number (Diaz & Cabido 2001). The idea that functional traits influence the outcome of community assembly is closely associated with the concept of ecological filters, were abiotic and biotic filters in combination with disturbance, environmental stress and competition influence which species establish (Fattorini & Halle 2004).

One of the first studies to show that functional traits influence the outcome of community assembly in restoration was done by Pywell et al. (2003). An important finding in this paper is that among forbs, traits influencing colonisation ability are important in the first year, but with time traits linked to competitive ability become more important for predicting the community assembly. Several other researchers have also demonstrated the value of functional diversity in understanding the processes that govern community assembly (Tilman et al. 1997, Diaz & Cabido 2001, Diaz et al. 2003). If functional diversity is included as a component in the assessment of restoration projects, we may be able to assess whether restoration through species introduction can successfully establish a community with a diversity of traits that are similar to the reference system. We may also gain a deeper understanding of which traits are important for species to establish and be able to determine before the introduction which species are likely to be filtered out.

Concluding remarks

Introduction of species has proven to be a useful tool in establishing species that are dispersal limited, as the reviewed data in this paper shows. Restoration of semi-natural grasslands often requires that target species are introduced due to the fact that they no longer exist in the seed bank, and dispersal from the nearest population is often improbable due to landscape fragmentation. Plug-planting may not be an ideal method for reintroducing a community in semi natural grasslands. In this ecosystem direct seeding or hay spread is achieved easier with satisfactory results. On the other hand using direct seeding in restoration of rare plants risks being a waste of seeds, and hence plug plants might be the best option. There is no silver bullet of restoration, and the method of introduction will have to be dependent on the species in question, as well as the size of the restoration area and the funding available.

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CHAPTER II

Vegetation recovery after multiple-site experimental fen restorations

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Vegetation recovery after multiple-site experimental fen restorations

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ABSTRACT

Large peatland areas have been drained for forestry and agricultural purposes, resulting in the decline of characteristic biodiversity. Two measures commonly suggested for restoring drained fens is ditch blocking and tree removal to raise the groundwater table and increase light availability, respectively. In 2002, we initiated factorial restoration experiments, including ditch blocking and tree removal, in three former rich fens that had been drained for forestry purposes. Species cover of vascular plants and bryophytes were monitored during 8 years in permanent plots along transects perpendicular to the ditch for all four treatment combinations. Both methods had positive and independent effects on the cover of wetland vegetation. Specifically, *Sphagnum* species and wetland bryophytes showed a persistent positive response to both clear cutting and rewetting. Wetland vascular plants and grasses showed a persistent positive response to clear cutting. Sedges and species number responded positively to both clear cutting and ditch blocking, but the response was partly transient, and for species richness the response was limited when restoration methods were applied separately. Rich fen indicators of vascular plants and bryophytes did not respond to any of the restoration treatments. This indicates that species introduction in combination with further habitat restorations may be necessary to re-establish the original rich fen flora. Nevertheless, we conclude that the combination of ditch blocking and clear cutting are effective measures to partly restore wetland vegetation on previously drained and forested fens, while peat subsidence along the ditch may restrict the success further away from ditches.

1. Introduction

During the last century, peatlands in Europe suffered from drainage conducted in order to increase agricultural and forestry production (Vasander et al., 2003). In the non-tropical world, 50% of the original peatland loss is due to drainage for agriculture, and 30% is due to drainage for forestry. The estimated loss of peatlands in Sweden during the 20th century for forestry production purposes is close to 1 million ha, corresponding to about 10% of the original peatland area (Rydin et al., 1999). In Sweden, only 20% of the extant peatland area is in a pristine state, with the rest being affected and disturbed (e.g. by partial drainage) (Gunnarsson and Löfroth, 2009). For other North-European countries the pattern is similar. 5.9 million ha of peatlands have been drained for forestry purposes in Finland. This is more than half the nation's original peatland area (Paavilainen and Päivänen, 1995). In Estonia, drainage of peatlands for peat-harvest, forestry and agriculture has resulted in that only 32% of the peatlands are regarded as pristine (Vasander et al., 2003). Restoration of drained peatlands is badly needed in protected areas (e.g. Sundberg, 2006). In this paper we focus on fens (peatlands with an inflow of water from the surrounding mineral soil), particularly rich fens (i.e. fens with high pH and calcareous water).

Drainage of peatlands changes the habitat conditions of plants, primarily by changing the hydrology but also by causing eutrophication (Turner and Haygarth, 2001) and acidification (Laine et al., 1995). Eutrophication is caused by the release of available nitrogen and phosphorous compounds from oxidizing peat and is followed by increased productivity and decreased light availability. Frequently, trees and shrubby species establish in response to the change in nutrient availability, imposing a further shading effect. In peatlands drained for forestry, this process is enhanced artificially by planting young trees. In such a situation, light deficiency is supposed to be the major cause of the decline of characteristic

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Nomenclature

Species names of vascular plants Mossberg and Stenberg (2003)
Bryophytes Hallingbäck et al. (2006)

fen species (Vermeer and Berendse, 1983; Fojt and Harding, 1995), which are reported to have low shade tolerance and competitive ability (Kotowski and van Diggelen, 2004). Moreover, with the growth of trees a further loss of water is expected because of increased transpiration (Jauhiainen et al., 2002).

Acidification is another indirect effect of fen drainage, caused by the accumulation of rainwater in the peat after drop of the groundwater level (van Diggelen et al., 2006). In result, peat mosses (*Sphagnum* spp.) usually expand in the community, which causes a positive feedback of further acidification because of ion exchange by these species (Rydin and Jeglum, 2006). Brown mosses connected to base-rich fens decline, either due to a direct effect of the lowered pH, or due to competition with acidity-tolerant species (Kooijman, 1992; Kooijman and Bakker, 1995; Granath et al., 2010).

To counteract the loss of original fen vegetation that is associated with habitat deterioration, restoration of fens focuses on re-establishing the original hydrological, trophic and light conditions. In heavily drained fens, topsoil removal is proposed as the most effective method to reduce fertility and increase moisture (Klimkowska et al., 2010), while in less severely drained sites blocking of drainage ditches and removal of trees and shrubs may suffice (Lanta et al., 2006; Mälson et al., 2008, 2010; Haapalehto et al., 2011; Laine et al., 2011). A combination of these two measures is especially recommended in peatlands drained for forestry, and has been widely utilized in a large peatland restoration program in Finland, including 16,000 ha of former drained peatlands (Aapala et al., 2009). However, there are no studies testing the relative effectiveness, or potential interactions, of these two measures in peatland systems. As drainage has frequently been done by crossing the mire with a single ditch, the only feasible option for restoring hydrology is to block water flow in the ditch. Such a measure has, however, a spatially divergent effect, because the surface is usually inclined towards the ditch as an effect of former subsidence (Minkkinen and Laine, 1998; Schipper and McLeod, 2002).

With this paper, we try to fill this gap, by presenting intermediate term effects from a multi-site restoration experiment, carried out in three drained and forested (former) rich fens in Sweden. We use a factorial design on the scale of 50 m × 150 m field plots to examine the spatial effects of ditch blocking and clear cutting, as methods to restore wetland vegetation within an 8 year observation period. From previously published results (Mälson et al., 2010) we hypothesized that wetland species, sedges, grasses and rich fen indicators of vascular plants and bryophytes would increase in response to rewetting and clear cutting, but that vegetation in adjacent untreated plots would not change substantially during the study period.

2. Methods

2.1. Site descriptions

In this study three drained rich fen sites in the province of Uppland, east-central Sweden were included: the extremely rich fen Severmossen (60°26'13.41"N, 17°57'34.65"E), and the former moderately rich fens Styggkärret (59°57'34.77"N, 17°18'20.25"E) and Ultunaviken (59°57'12.74"N, 17°18'21.19"E) (Fig. 1). Mean temperature from the nearby meteorological station in Uppsala is −4.2 °C in January, and 16.4 °C for July. Annual precipitation is 544 mm (SMHI, 2005).

All three sites were drained during the 1950s and were then spontaneously colonized by *Betula pubescens*, *Pinus sylvestris* and *Picea abies*. Pre-drainage vegetation at Styggkärret and Ultunaviken included several indicators of moderately rich fens, for example the brown mosses *Scorpidium scorpioides*, *Scorpidium cossonii*, and *Campylium stellatum*, and the vascular plants *Eriophorum latifolium* and *Pedicularis sceptrum-carolinum* (von Krusenstjerna, 1945; Almquist, 1965). It was *a priori* known that Severmossen had much less *Sphagnum* than the other two sites, although peat stratigraphy shows that *Sphagnum* section Squarrosa had been present in Severmossen historically. The same peat stratigraphy of the three sites indicates that all three sites were rich fens prior to drainage (C. Greiser, unpublished). Measurements of von Post humification (Rydin and Jeglum, 2006) indicate that in 5 out of 9 cores the peat at 20 cm is more decomposed than at 50 cm depth, which is a likely effect of drainage (C. Greiser, unpublished). Topography measurements of all sites showed that the peat surfaces were trough-like, and inclined towards the ditch by 0.10°, 0.43° and 0.27° over a distance of 32 m perpendicular to the ditch at Severmossen, Styggkärret and Ultunaviken, respectively. The steepest inclination occurs close to the ditch.

2.2. Restoration measures and experimental design

All three sites underwent the same restoration treatments during December 2002 to June 2003 (Fig. 2). Three dams were placed along the upper 150 m of the ditch, 50 m apart, with the last dam in the middle of the restoration site. The dams were made by sheet piled wood with a 2–3 m long plug of peat and mineral soil deposited upstream of the dam. The wooden dam was driven in at least 0.5 m below the bottom of the ditch and 0.5–1 m into the sides, with the top level with the surrounding ground. All trees were cut and removed on 1.5 ha (50 m × 300 m) along one side of the ditch, while trees were kept on the opposite side (Fig. 2). This created four field plots (50 m × 150 m) per site, and a factorial design with respect to the restoration treatments rewetting (rewetted vs. drained) and tree removal (clear cut vs. forested).

In each field plot four transects were located perpendicular to the ditch, with a distance of 30 m between transects. Permanent plots of 0.5 m × 0.5 m were systematically established at observation points located 4, 8, 16, 24 and 32 m from the ditch in each transect (Fig. 2). Tall hummocks were excluded from the sampling, as vegetation in this habitat is expected to be marginally affected by water level change (cf. Økland, 1986). To quantify small scale variation, two additional permanent plots were located adjacent to the central plot at each observation point in the rewetted and clear cut field plots (Fig. 2). This resulted in an experiment where each site was represented by 120 permanent plots distributed over 80 observational points, along 16 transects within 4 field plots.

2.3. Response variables

In each permanent plot vegetation was monitored annually from 2002 (pre-treatment) until 2005, and then in 2010. The cover

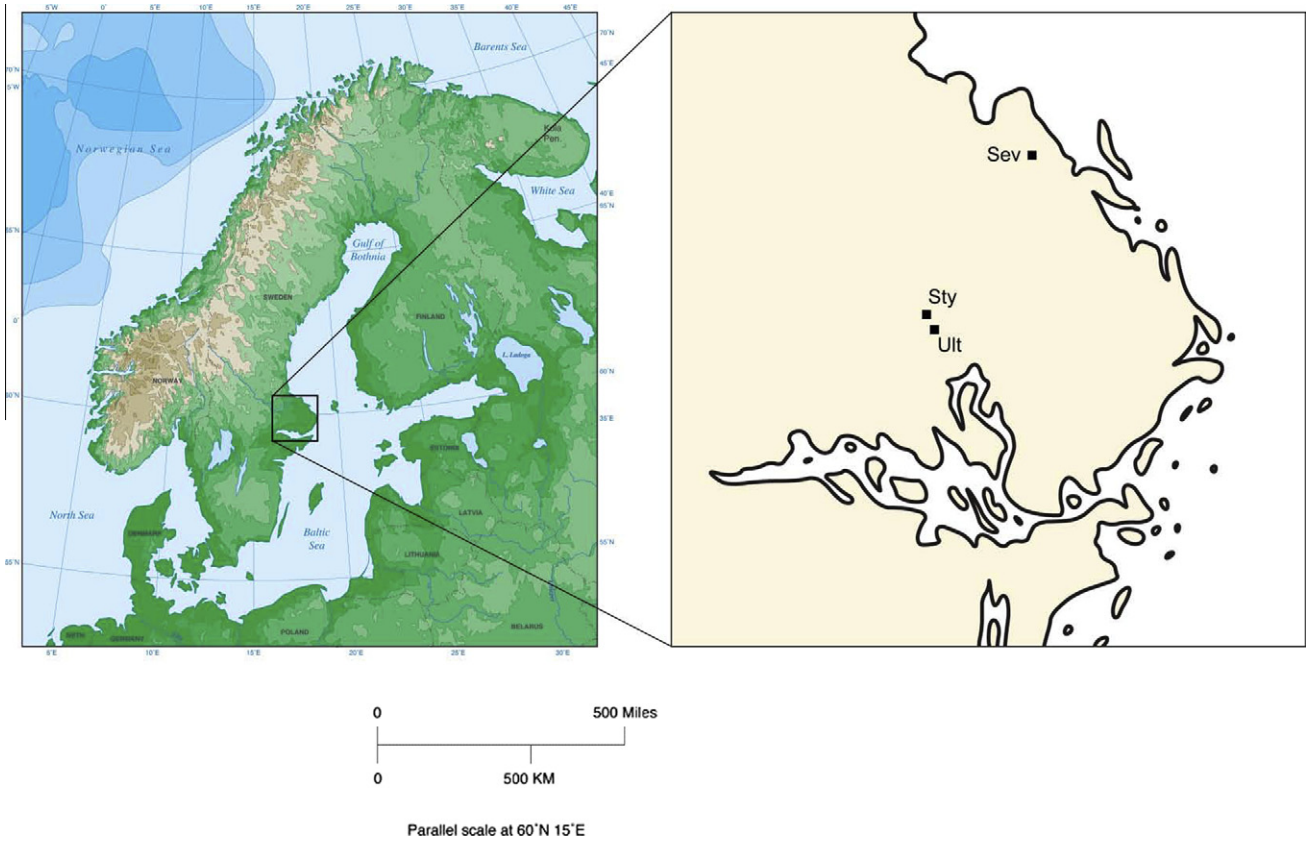

Fig. 1. Location of the restoration sites Severmossen (Sev), Styggkärret (Sty) and Ultunaviken (Ult) in east-central Sweden.

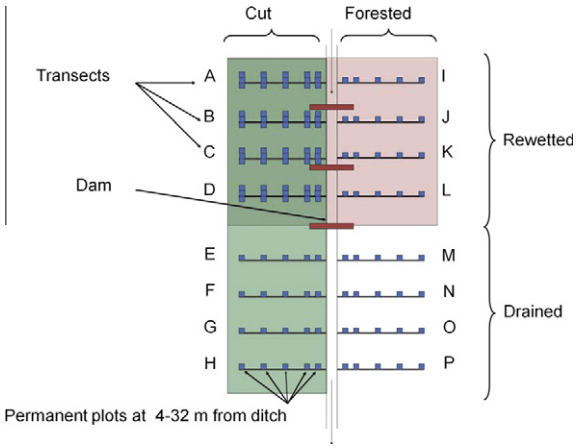

Fig. 2. Outline of the experimental and sampling design for each of the three sites.

of each species of vascular plant and bryophyte was estimated with 1% resolution. Species below 1% of cover were estimated with 0.1% accuracy by using a high resolution grid frame. Twelve observations were excluded from the analysis due to damage done by thinning operations or loss of plot markers.

Species were classified into functional groups hypothesized to respond positively to the restoration treatments. Thus the vegetation response was examined with respect to the cover of sedges, grasses, *Sphagnum* species, wetland vascular plants, wetland bryophytes , rich fen indicators of vascular plants and rich fen indicators of bryophytes (excluding *Sphagnum*), and the total species number. For reference the cover and frequency for each observed species and their classification with respect to the above functional group is listed in Appendix A. Species turnover was calculated as Bray–Curtis dissimilarity index (Bray and Curtis, 1957) in relation to the starting year, shown across sites and treatments and in relation to distance from the ditch.

Piezometers were inserted in the center of each permanent plot, and water levels were recorded twice prior to the restoration in 2002 and once after the restoration in 2003.

2.4. Statistical analysis

Vegetation response to the restoration treatments were examined with a mixed linear model (Proc Mixed, SAS 9.1, SAS Institute Inc., Cary, NC, USA; Littell et al., 2002). In the analysis, site (Sev, Sty, Ult), rewetting (rewetted, drained), tree removal (clear cut, forested), distance along the ditch with scale restarting at each treatment quadrant (30, 60, 90, 120 m), distance from ditch (4, 8, 16, 24, 32 m) and selected interactions between these effects (see below) were treated as fixed class variables. Time (2002, 2003, 2004, 2005, 2010) was also treated as a fixed factor, and all interactions between time and the other fixed factors was included in the model. Thus the structure of the fixed effects of the statistical model was:

$$y_{abcdef} = S_a + \mathrm{Rw}_b + \mathrm{TR}_c + (\mathrm{Rw}\times\mathrm{TR})_{bc} + \mathrm{Time}_d + (S\times\mathrm{Time})_{ad} + (\mathrm{Rw}\times\mathrm{Time})_{bd} + (\mathrm{TR}\times\mathrm{Time})_{cd} + (\mathrm{Rw}\times\mathrm{TR}\times\mathrm{Time})_{bcd} + \mathrm{DA}_e + (\mathrm{Rw}\times\mathrm{DA})_{be} + (\mathrm{DA}\times\mathrm{Time})_{ed} + (\mathrm{Rw}\times\mathrm{DA}\times\mathrm{Time})_{bed} + \mathrm{DF}_f + (\mathrm{Rw}\times\mathrm{DF})_{bf} + (\mathrm{TR}\times\mathrm{DF})_{cf} + (\mathrm{DF}\times\mathrm{Time})_{fd} + (\mathrm{Rw}\times\mathrm{DF}\times\mathrm{Time})_{bfd} + (\mathrm{TR}\times\mathrm{DF}\times\mathrm{Time})_{cfd}$$

where y_{abcdef} refers to the vegetation cover predicted from systematic variation due to site, combination of restoration treatments and

spatial variation due to distance from ditch block and distance from ditch. The capital letter on the right hand side represents the fixed effects of as follows; *S* refers to the a'th Site, Rw to the b'th Rewetting treatment, TR to the c'th tree removal treatment, RW × TR to bc'th interaction between rewetting and tree removal treatment, Time to the d'th time, *S* × Time to the ad'th interaction between site and time, Rw × Time to the bd'th interaction between rewetting and time, TR × Time to the cd'th interaction between tree removal and time, Rw × TR × Time the bcd'th interaction between rewtting, tree removal and time, DA the e'th distance along the ditch, Rw × DA the be'th interaction between rewetting and distance along ditch, DA × Time the ed'th interaction between distance along ditch and time, Rw × DA × Time the bed'th interaction between rewetting, distance along the ditch and time, DF the f'th distance perpendicular from the ditch, Rw × DF is the bf'th interaction between rewetting and distance from the ditch, TR × DF the cf'th interaction between tree removal and distance from the ditch, DF × Time is the fd'th interaction between distance from the ditch and time, Rw × DF × Time is the bfd'th interaction between rewetting, distance from ditch and time, and TR × DF × Time is the cfd'th interaction between tree removal, distance from ditch and time.

The 150 m × 50 m experimental field plot, the transects (within field plots) and the observational points (within transect) were treated as random variables, as were the interactions of time with field plot, transect and observation point.

To test the hypothesis that vegetation responded over time in the restored plots, but not in the untreated plots, we contrasted observed data against the null hypothesis of no vegetation response over time (H_0: $y_{t1} = y_{t2} = y_{t3} = y_{t4} = y_{t8}$). That is, under the null hypothesis all differences in vegetation cover observed between years could be attributed to natural random variation. The probability of the outcome in the observed data under the null hypothesis was then quantified for treated (clear cut or rewetted) and untreated field plots separately. In practice this was achieved by splitting the interactions between time and treatments with the LSMeans/slice option in Proc Mixed. The level of replication for these tests was time within field plot ($N = 5 \times 12 = 60$), and thus the experimental design on this level was similar to a split plot design, with restoration treatments (RW, TR) as factorial main plot factors, and vegetation response to treatment (Rw × Time, TR × Time) as a split plot factors.

Residuals at the split plot level (Field plot × Time) were tested for normality with the Anderson–Darling test. Response variables with a skewed residual distribution were square root or log (ln [$y + 0.1$]) transformed to achieve approximate normal distributions.

As eight response variables were tested, we used a simple Bonferroni correction to control the family α-level to 0.05. Thus the threshold for statistical significance after correction for multiple testing was adjusted to 0.00625 ($=0.05/n_y$).

3. Results

3.1. Vegetation response to tree removal (TR)

The cover of Sedges, Grasses, *Sphagnum* and wetland vascular plants and wetland mosses all showed a positive response to clear cutting ($p < 0.001$), but did not change significantly in the forested plots over the observation period ($p > 0.41$) (Table 1, Fig. 3a–e). In specific, after 8 years *Sphagnum* had increased from 10% to 15% cover, wetland bryophytes from 27% to 37%, wetland vascular plants from 28% to 36%, and grasses from 2.4% to 4.2%. The response in sedges was strongly affected by clear cutting ($p < 0.0001$). However, the effect was partly transient with an increase in cover from 0.7% to 5.1% after the first 3 years, followed by a decline to 3.4% by the end of the study period (Fig. 3e). There was a similar tendency in the untreated plots, but here the changes over time was within the expectations from natural random variation ($p = 0.19$). Species richness also responded to clear cutting during the observation period ($p < 0.001$), and increased from an average of 8.5–12 species during the first 3 years of the experiment (Fig. 3f). There was a similar increase in the forested plots during the three initial years after the restoration efforts ($p = 0.006$), and the number of species increased from 7 to 9 in the untreated plots. Thus it is possible that the initial increase in species richness in the clear cut plot was not exclusively due to the restoration efforts. However, after an additional 5 years the species richness had dropped down to the original level in the untreated plots (7 species), whereas it had stabilized around 11 species in the clear cut plots.

3.2. Vegetation response to rewetting (Rw)

The cover of *Sphagnum* and wetland bryophytes showed a positive response to rewetting ($p < 0.002$), but did not change significantly in the plots which remained drained over the observation period ($p > 0.50$) (Table 1, Fig. 3a and b). The response in sedges was also affected by rewetting ($p < 0.001$). As noted in the response with respect to clear cutting (above), the effect was most pronounced after 3 years when the cover had increased from 0.8% to 4.2%, whereas it had dropped to 3.3% cover after 8 years. There was also a tendency towards a response in the drained plots ($p = 0.01$). However, this was primarily due to the response in the clear cut drained plots, as the cover of sedges in the drained and forested plots was stable at 0.5% (Fig. 3e). Species richness showed

Table 1
Vegetation responses to two wetland restoration methods. For each functional group, mean cover, transformation used and test of normality are listed together with test statistics and *p*-values for a response (change) during the investigation period. For each restoration method (clear cut and rewetting) the response in the treated plots (left) are compared to the response in untreated plots (Ctrl, right).

Taxa	Mean cover (%)	Transform	Test of normality[a]	Response to tree removal				Response to ditch blocking			
				Clear cut		Forest (Ctrl)		Rewetted		Drained (Ctrl)	
			p-Value	$F_{4,24}$[b]	*p*-Value	$F_{4,24}$	*p*-Value	$F_{4,24}$	*p*-Value	$F_{4,24}$	*p*-Value
Sphagnum	19	None	0.18	6.7	0.0009	1.03	0.41	7.03	0.0007	0.86	0.50
Wetland bryophytes	27	None	>0.25	7.06	0.0007	0.39	0.81	5.63	0.002	0.8	0.54
Wetland vasc plants	24	None	>0.25	6.31	0.001	0.44	0.78	3.23	0.03	1.81	0.16
Grasses	1.7	ln($y + 0.1$)	>0.25	6.3	0.001	0.25	0.91	3.01	0.04	1.19	0.34
Sedges	2.2	sqrt	>0.25	31.5	<.0001	1.69	0.19	22.98	<.0001	3.99	0.01
RF ind brown mosses[c]	0.10	ln($y + 0.1$)	0.10	2.06	0.12	0.06	0.99	1.9	0.14	0.6	0.67
RF ind vasc plants[c]	0.07	ln($y + 0.1$)	>0.25	1.42	0.26	0.19	0.94	1.26	0.31	0.72	0.59
Species number	10	ln($y + 0.1$)	0.23	11.98	<.0001	7.23	0.0006	9.2	0.0001	9.46	<.0001

[a] Anderson–Darling test of residual distribution.
[b] *F*-ratio from contrasts of change (Time) with 4 (numerator) and 24 (denominator) degrees of freedom.
[c] RF ind = Rich fen indicators.

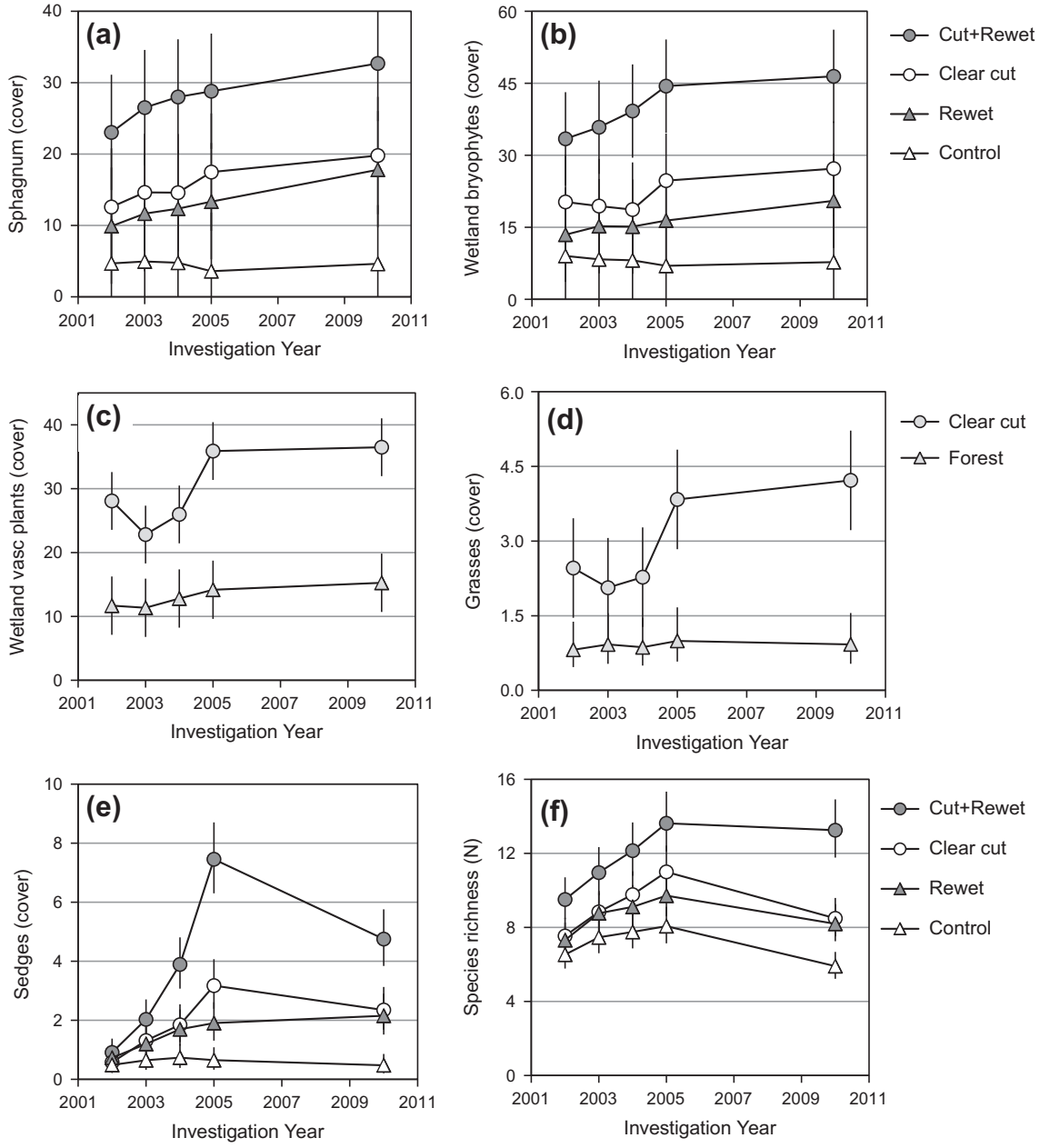

Fig. 3. Development (mean ± SE) between 2002 and 2010 of: (a) the cover of *Sphagnum*, (b) wetland bryophytes, (c) wetland vascular plants, (d) grasses, (e) sedges, (f) species richness; according to significant treatments effects and their controls.

a strong transient response both in drained and rewetted plots ($p = 0.0001$). However, whereas the average number in the drained plots after 8 years were similar to those at the start of the experiment (7.0 vs. 7.1 respectively), there was a tendency towards an overall increase in the number of species in the rewetted plots (8.3 vs. 10.4).

The effects of clear cutting appeared to have affected the vegetation primarily independently of the effect of rewetting, as indicated by a non-significant interaction effect between the treatments and time (Rw × TR × Time, $p > 0.54$, data not shown).

3.3. Spatial and temporal limitations of treatment effects

There was strong and systematic spatial variation in vegetation cover within the field plots. This variation was primarily related to the distance from the ditch, as indicated by significant DF or DF × Time effects for all examined response variables ($p < 0.01$, data not shown). This systematic spatial variation was taken into account in the analysis by using distance from ditch and its interaction with time as a blocking factor.

Ditch blocking caused the water level to increase on average by 25 cm at four meters from the ditch between 2002 and 2003, whereas the increase was limited to 12 cm at 32 m (Fig. 4a; Rw × DF × Time, $p < 0.0001$, data not shown). In the drained treatment, we could still observe an indication of drainage, with changes in water level being more negative near the ditch. The difference in the drained treatment was however marginal compared to the same comparison in the rewetted treatment.

As we expected the change in water level to be the driving factor for the vegetation response to ditch blocking, we examined to what extent the observed rewetting response of *Sphagnum*, wetland bryophytes, sedges and species richness depended on the dis-

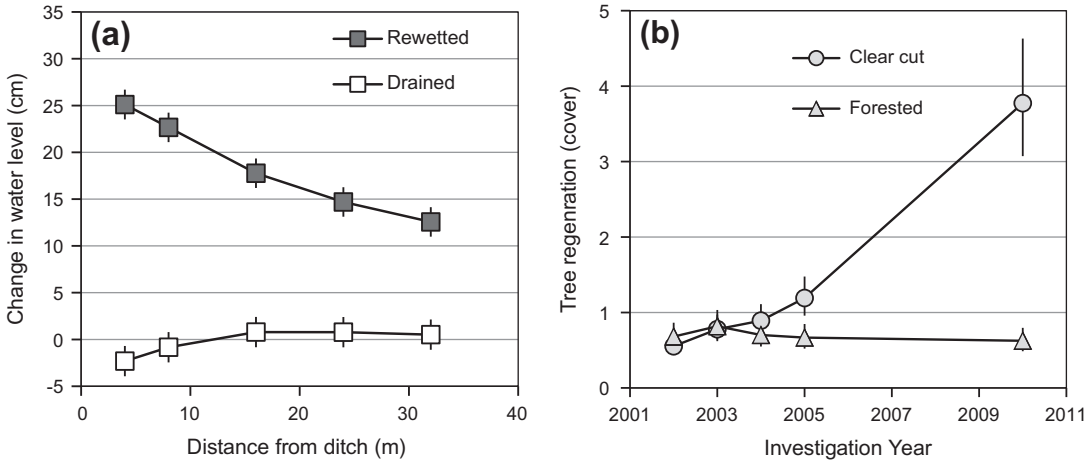

Fig. 4. (a) The effect of distance from the ditch (mean ± SE) on water level change, in the rewetted and drained treatments. (b) Change in juvenile tree cover in relation to the cutting treatment.

tance from the ditch. This analysis showed that the response in sedges followed that of the water level, with a much stronger response 4 m from the ditch than at 32 m. A similar but weaker trend was observed for species richness, where the *F*-ratios for the response in the rewetted plots dropped from 28.6 to 4.0, and from 10.7 to 6.4 for sedges and species richness, respectively. However, the response in *Sphagnum* and wetland bryophytes showed no such trends, suggesting that the rise of water level was sufficient in all of the plots for the observed positive response with respect to these bryophytes.

Tree regeneration strongly increased with clear cutting ($p < 0.0001$, data not shown) and the cover of juvenile trees had increased from 0.6% to 3.8% at the end of the 8 year observation period (Fig. 4b). To test whether the decrease in sedges and species richness observed in the clear cut plots coincided with an increase in tree cover, tree cover (nested within year) was introduced as a covariate in a separate analysis of the clear cut plots. We found a negative correlation between species richness and tree cover for 2010 ($p = 0.009$), that could account for approximately half of the decline in species number observed between 2005 and 2010. However the correlation between cover in sedges and trees was not statistically significant and an increased cover of juvenile trees could not explain the decline in sedges observed at the end of the experiment.

Species turnover across all sites and treatments changed most rapidly during the first year (19% in Bray–Curtis dissimilarity index) and then the rate declined successively such that after 8 years the cumulative change was 38%. After 8 years species turnover was 56 ± 14% (mean ± SE) at 4 m from the ditch in the rewetted parts, while it was 32–39 ± 9–13% at all other distances in both the rewetted and drained parts.

4. Discussion

In line with our hypothesis, our results show that both methods of peatland restoration had a positive and independent effect on the cover of wetland vegetation, and that species richness increased with time after the restoration efforts. However, the response to clear cutting and rewetting by ditch blocking varied among functional groups, and contrary to our hypothesis the measures taken were not sufficient to restore rich fen species within 8 years.

Restoration experiments are usually restricted to one site. We acknowledge the heterogeneity in starting conditions among our sites, but we stress that results from a multi-site study are more generally valid. An example of site-specific response was the strong decrease in grasses at Severmossen immediately after the restoration measures. The different response at Severmossen is due to a large cover of *Molinia caerulea* close to the ditch in 2002, while it was absent or rare at the other two sites. *Molinia* decreased at Severmossen from 17% to 13%, during the first year of restoration, probably in response to water logging (Armstrong and Boatman, 1967; Taylor et al., 2001; Mälson et al., 2008).

4.1. Rewetting and tree removal

Overall, both treatments appeared successful in recreating functional, peat-forming peatland ecosystems, especially when applied in combination over a longer time period. The increase in *Sphagnum*, sedges and other wetland plants, as well as species richness were clear indications of the positive responses. In a study over 4 years on rewetting of spruce mires, Laine et al. (2011) noted a significant response only in sedges and mire dwarf shrubs. In the only other longer term (10 years) study published on the vegetation responses of rewetting and tree removal, Haapalehto et al. (2011) also noted a strong increase in *Sphagnum* and other peatland plants. However, hummock and lawn species responded positively while species dependent on the wettest hollows and minerotrophic species were often absent (Haapalehto et al., 2011; Laine et al., 2011). We did not particularly test the different habitat groups of *Sphagnum*, but minerotrophic species responded similarly to less mineral-demanding species. However, species of the wet hollows were rare, indicating that our restoration promoted primarily species of hummocks and lawns (upper parts of hollows).

The decline of sedges after some years of rapid increase may seem surprising, but has been observed in other studies (Mälson et al., 2008; Haapalehto et al., 2011). Possible reasons for this pattern may be the simultaneous increase of more competitive juvenile trees, peat mosses and grasses. The species showing the most dramatic decline from 2005 to 2010 was *Carex canescens*, a species that appears weakly competitive and ruderal (it often colonizes bare peat).

4.2. Temporal and spatial limitations of restoration methods

One of the challenges after restoration by tree removal is to maintain the open area and avoid reestablishment of trees (Aapala

et al., 2009). We saw a clear trend of encroachment by birch and pine saplings in the cut treatments between year 3 and 8. No mature trees were observed to die from the rewetting treatment at the forested side, which indicates that additional thinning will be necessary to maintain the positive effects of the open conditions.

The decrease in water level elevation with increasing distance from the ditch in the rewetted area, shows that there is a spatial limitation of the hydrological restoration. At 32 m from the ditch the rise in water level was much less than at 4 m from the ditch. The combined negative effect of distance from the ditch in the rewetted treatment on species turnover, species richness and sedge cover, indicates that the higher water level near the ditch created more suitable conditions for characteristic fen species there than further away. Also, initially the water level was lowest close to the ditch. This in turn resulted in a higher turnover of species, when less adapted species were replaced by species more adapted to the new conditions.

The problem to restore hydrology over large areas in trough-like, drained peatlands, can be approached in two ways: (1) dams have to be made higher and much wider to raise the water table over larger areas (with the effect that areas close to the ditch will be much more inundated than in an original state); or (2) drained peatlands may be improved and partly restored by these simple, low and cheap dams, with the opportunity to reduce the risk of flooding surrounding productive forests or arable land.

Besides from the conservation gains, damming of peatlands also leads to conservation of water in the landscape and slows water runoff from land areas. In the case of our three fens, the average water-storage capacity in the hydrologically restored parts was approximately 670 m^3 water ha^{-1} more than in the still drained parts, given the values from the ditch and up to 32 m away, and that water occupies half the peat volume.

4.3. Lack of response in rich fen species

We note that, rich fen indicators, which were one of the targets of our restoration, did not react to the hydrological measures. Previous studies also reported that, while a rising groundwater level can help to re-establish wetland plants, the return of rich fen specialists often fails (Mälson et al., 2010). The reason may be that inundation of degraded peat soils leads to the mobilization of N and P (Broll et al., 2002; Zak et al., 2010), favoring a few highly-competitive and shading species. Another explanation is the irreversibility of wetland drainage: the resilience of degraded fen ecosystems after the development of tussock-forming sedges and grasses or hummock-forming peat mosses (Klötzli and Grootjans, 2001) hampers their return to the mesotrophic rich fen stage. Also a lowering of the pH (at two of the sites) and establishment of *Sphagnum* may hamper the recolonization of rich fen indicators (Paulissen et al., 2004; Mälson et al., 2010). In another study on the effects of shrub removal in a rich fen, cover and species richness of rich fen indicators increased markedly during 6 years (Sundberg, in press). The discrepancy between our study and the one by Sundberg may be that in the latter site degradation was not as severe, rich fen indicators were abundant nearby, and that grazing cattle acted as dispersers and topsoil disturbers that facilitated reestablishment. Altogether, drainage of rich fens may inevitably result in a speed-up of natural peatland succession that is difficult to counteract.

Although the lack of species response has been reported previously in shorter-term studies (Mälson et al., 2010), we did expect larger changes after 8 years. In line with earlier experiences (Mälson and Rydin, 2007. Rochefort et al., 2003; Hedberg and Kotowski, 2010; Klimkowska et al., 2010; Mälson et al., 2010) it seems often necessary to combine ditch blocking and tree removal with ground disturbance and species introduction in order to successfully restore the complete rich fen vegetation in deteriorated sites.

4.4. Conclusions

As hypothesized, our study shows that restoration by ditch blocking and tree removal can be effective methods for restoring the hydrology and openness, and a functional vegetation, in peatlands drained for forestry. Species richness, wetland bryophytes and sedges responded independently and positively to both rewetting and tree removal, and increased most in the combined treatment, suggesting that both treatments should be applied in attempts to restore fens. Wetland vascular plants and grasses responded only to tree removal. Although the lack of response in typical rich fen species has been reported in short-term studies, we did hypothesize larger changes after 8 years. It seems necessary to combine ditch blocking and tree removal with ground disturbance and species introductions in order to successfully restore the complete rich fen vegetation.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2012.01.039.

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Appendix A. Registered species, their average cover and plot frequencies (out of 120 plots) across all treatments at the three (former) rich fen sites during 2002-2010, and their classification into functional/ecological groups. Empty cells are shown for species that were not recorded in any plot in any year at the site. G, grasses; H, herbs; RI, rich fen indicators; S, sedges; SP, *Sphagnum*; T, juvenile trees; WV,wetland vascular plants ; WB, wetland bryophytes.

Species		Severmossen										Styggkärret										Ultunaviken									
	Group	2002		2003		2004		2005		2010		2002		2003		2004		2005		2010		2002		2003		2004		2005		2010	
		Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq
Vascular plants																															
Agrostis canina	G, WV	0.02	2	0.01	1	>0.00	1	>0.00	1	0.00	0	1.30	29	1.93	30	3.02	30	3.64	48	4.98	46	1.63	16	1.94	18	1.84	15	2.28	19	0.33	14
Agrostis stolonifera	G, WV											0.01	1	0.01	2	0.14	2	0.09	3	0.28	1										
Alnus glutinosa	T, WV											0.17	1	0.05	1	0.46	1	0.06	1	0.01	1										
Andromeda polifolia	WV	0.56	41	0.47	40	0.40	46	0.41	47	0.28	35	0.08	1	0.03	1	0.01	2	0.05	2	0.03	2	0.70	24	0.62	23	0.55	24	0.66	28	1.26	28
Betula pubescens	T, WV	0.74	28	0.40	43	0.53	55	1.04	59	2.65	63	0.55	16	1.14	81	2.10	74	3.10	69	5.94	69	0.16	20	0.52	62	0.95	58	1.52	50	2.78	58
Calamagrostis arundinacea	G	0.09	3	0.03	2	0.02	2	0.03	3	0.00	0	0.08	1	0.08	1	0.04	1	0.06	1	0.06	1										
Calamagrostis arundinacea x *canescens*	G, WV	0.30	3	0.16	5	0.20	4	0.17	4	0.00	0																				
Calamagrostis canescens	G, WV											0.34	4	0.38	4	0.16	4	0.26	6	0.47	7	0.18	5	0.22	4	0.23	4	0.29	4	0.20	4
Calamagrostis epigeios	G	1.06	18	0.60	24	0.62	32	0.83	35	0.65	27	0.00	0	0.00	0	0.00	0	0.00	0	0.01	1	0.02	2	0.03	2	>0.00	1	>0.00	1	0.00	0
Calamagrostis purpurea	G, WV	0.00	0	0.01	1	0.00	0	0.00	0	0.00	0	0.03	4	0.11	3	0.41	5	0.66	6	0.83	25										
Calamagrostis stricta	G, WV	0.00	0	0.00	0	0.00	0	0.00	0	>0.00	1	0.00	0	0.04	1	0.07	1	0.05	1	0.00	0										
Calluna vulgaris		0.36	12	0.28	13	0.27	13	0.22	13	0.22	14	0.00	1	0.01	1	0.02	1	0.01	1	0.00	0	0.00	0	0.01	1	0.01	1	0.01	1	>0.00	1
Cardamine pratensis ssp. *paludosa*	WV	0.00	0	0.00	0	>0.00	1	>0.00	1	0.00	0																				
Carex canescens	S, WV											0.10	3	0.20	4	1.07	16	4.30	27	1.03	20	0.01	1	0.05	2	0.08	3	0.12	4	0.01	3
Carex chordorrhiza	S, WV	0.00	0	0.00	0	>0.00	1	>0.00	1	0.02	1	0.17	14	0.28	22	0.49	22	1.11	26	2.01	31	0.24	15	0.40	17	0.39	17	0.41	19	0.60	20
Carex demissa	S, WV	0.00	0	0.00	0	>0.00	2	0.01	2	0.00	0																				
Carex dioica	S, WV	0.00	0	0.03	3	0.13	3	0.08	3	>0.00	1	0.01	2	0.01	3	0.02	2	0.01	3	0.03	5	0.41	42	0.67	51	0.75	51	0.91	53	0.76	43
Carex echinata	S, WV											0.23	3	0.34	6	0.90	11	1.45	16	0.88	24	0.42	8	0.74	11	0.86	10	0.90	13	0.16	10
Carex elata	S, RI, WV											0.00	0	0.00	0	0.00	0	0.05	1	0.03	1										
Carex flava	S, R, WV I											0.00	0	0.01	1	>0.00	2	0.08	4	0.03	3										
Carex hostiana	S, RI, WV	0.03	3	0.04	3	0.04	5	0.13	15	0.04	8																				
Carex lasiocarpa	S, WV											0.50	29	0.79	33	1.59	39	3.13	46	1.31	60	0.56	28	0.87	45	0.96	49	1.72	60	1.24	57
Carex livida	S, WV											0.00	0	0.00	0	>0.00	1	>0.00	2	0.00	0	0.00	0	>0.00	1	>0.00	1	>0.00	1	0.00	0
Carex magellanica	S, WV											0.00	0	0.00	0	0.00	0	0.01	1	0.00	0										
Carex nigra	S, WV	>0.00	1	>0.00	1	0.01	1	0.01	1	0.00	0																				
Carex panicea	S, WV	0.28	36	0.73	55	0.88	56	1.22	56	0.71	48	0.15	3	0.19	5	0.32	6	0.36	11	0.30	10										
Carex pauciflora	S, WV																					0.00	0	>0.00	1	>0.00	1	0.03	1	0.04	1
Carex pulicaris	S, RI, WV	>0.00	1	0.00	0	0.00	0	0.01	1	0.00	0																				
Carex rostrata	S, WV	0.00	0	0.00	0	0.00	0	0.00	0	0.02	1	0.00	2	0.04	3	0.05	3	0.06	4	1.34	15	0.88	28	1.08	29	1.05	37	2.14	49	1.63	39

Species		Severmossen										Styggkärret										Ultunaviken									
	Group	2002		2003		2004		2005		2010		2002		2003		2004		2005		2010		2002		2003		2004		2005		2010	
		Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq
Carex viridula	S, WV																					0.00	0	0.00	0	>0.00	1	>0.00	1	0.00	0
Cerastium fontanum												0.00	0	0.00	0	0.00	0	0.01	2	>0.00	1										
Cirsium arvense		0.00	0	0.00	0	0.00	0	0.00	0	0.01	1	0.00	0	0.00	0	0.00	0	0.08	1	0.00	0										
Cirsium helenioides	WV	0.00	0	0.00	0	0.00	0	0.00	0	0.01	1																				
Cirsium palustre	WV	0.13	19	0.06	16	0.09	17	0.17	20	0.04	9	0.05	3	0.01	4	0.02	3	0.03	2	0.20	11	0.00	0	>0.00	1	>0.00	1	>0.00	1	0.09	2
Comarum palustre	WV											0.14	2	0.38	2	0.75	2	0.28	3	0.22	4										
Corallorhiza trifida	WV	0.00	0	>0.00	1	0.00	0	0.00	0	0.00	0																				
Dactylorhiza incarnata	RI, WV											0.00	0	>0.00	1	0.00	0	0.00	0	0.00	0										
Deschampsia cespitosa	G, WV											0.01	1	>0.00	1	0.00	0	0.16	2	0.02	1	0.03	1	0.04	1	0.13	2	0.25	2	0.10	2
Deschampsia flexuosa	G											0.01	1	0.00	2	0.00	2	0.01	2	0.01	1	0.00	1	0.01	2	0.00	2	>0.00	2	0.00	0
Drosera intermedia	WV																					0.00	0	0.00	0	0.00	0	0.00	0	>0.00	1
Drosera rotundifolia	WV											>0.00	2	0.02	2	0.02	3	0.03	3	0.03	3	0.24	26	0.25	35	0.41	39	0.35	40	0.19	25
Dryopteris carthusiana												0.16	3	0.02	1	>0.00	1	0.01	1	0.01	1	0.10	2	0.04	2	0.03	2	0.03	2	0.05	2
Eleocharis quinqueflora	S, RI, WV	0.00	0	0.00	0	>0.00	1	>0.00	1	0.00	0																				
Empetrum nigrum	WV	0.10	8	0.06	7	0.05	6	0.07	7	0.08	5																				
Epilobium adenocaulon	WV											0.00	0	0.00	0	0.00	0	0.05	10	>0.00	1										
Epilobium angustifolium		0.00	0	0.00	0	0.00	0	>0.00	1	0.00	0																				
Epilobium palustre	WV											0.01	1	0.01	1	0.01	2	0.02	10	0.06	9	>0.00	1	>0.00	1	0.00	0	>0.00	1	0.00	0
Epipactis palustris	RI, WV	0.10	4	0.06	4	0.08	7	0.10	11	0.10	8																				
Equisetum fluviatile	WV											>0.00	2	0.01	2	0.03	3	0.13	6	0.05	16	>0.00	1	>0.00	1	>0.00	2	>0.00	1	0.02	2
Equisetum palustre	WV	0.01	1	0.01	1	>0.00	1	>0.00	1	0.00	0																				
Equisetum variegatum	RI, WV	0.00	0	0.00	0	0.00	0	>0.00	1	0.00	0																				
Eriophorum angustifolium	S, WV	0.00	0	>0.00	1	0.00	0	0.00	0	0.00	0	0.50	16	0.66	19	1.69	28	2.11	25	1.63	29	1.35	51	2.81	63	3.96	71	3.23	62	1.90	52
Eriophorum vaginatum	S, WV											>0.00	1	>0.00	1	>0.00	1	>0.00	1	0.00	0	0.23	9	0.33	13	0.63	15	1.28	17	1.31	16
Festuca ovina	G	>0.00	1	>0.00	1	0.00	0	0.00	0	0.00	0	0.03	1	0.01	1	0.01	1	0.01	1	>0.00	1										
Filipendula ulmaria		0.03	1	0.03	1	0.03	1	0.04	1	0.03	1																				
Fragaria vesca		0.19	5	0.24	5	0.19	5	0.16	4	0.00	0																				
Frangula alnus	WV T	0.04	1	0.02	5	0.02	8	0.02	8	0.07	11	0.00	0	0.01	1	0.03	1	0.03	1	0.01	1	0.07	1	0.02	2	>0.00	1	0.00	0	0.00	0
Galium boreale		0.02	1	0.02	1	0.02	1	0.01	1	0.01	1																				
Galium palustre	WV											0.01	2	0.04	2	0.26	6	0.19	8	0.30	16	0.01	1	0.04	1	0.05	1	0.02	2	0.00	1
Galium uliginosum	WV	0.00	0	0.00	0	0.00	0	>0.00	1	0.00	0																				
Geum rivale		0.04	1	0.03	2	0.04	2	0.01	3	>0.00	1																				
Gymnadenia conopsea	RI, WV	0.05	5	0.01	2	>0.00	1	>0.00	2	>0.00	1																				
Gymnocarpium dryopteris												0.00	0	0.00	0	0.00	0	0.00	0	0.01	1										
Hieracium sp.		0.00	0	0.00	0	>0.00	1	0.00	0	0.00	0																				
Huperzia selago	WV											0.01	2	0.00	0	0.00	0	0.00	0	0.00	0	0.01	1	0.01	1	0.01	1	0.01	1	0.01	1
Juncus bufonius	WV											0.00	0	0.00	0	0.00	0	>0.00	1	0.00	0										

Species		Severmossen										Styggkärret										Ultunaviken									
	Group	2002		2003		2004		2005		2010		2002		2003		2004		2005		2010		2002		2003		2004		2005		2010	
		Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq
Juncus conglomeratus	WV											0.00	0	0.00	0	0.00	0	0.00	0	0.02	1										
Juncus effusus	WV											0.00	0	0.00	0	0.00	0	0.00	0	0.05	3										
Juniperus communis	T	0.00	0	0.00	0	0.01	1	>0.00	1	0.24	2											>0.00	1	>0.00	1	>0.00	1	0.00	0	0.00	0
Larix decidua	T	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	>0.00	1	0.00	0	0.00	0										
Linnaea borealis		0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.00	0										
Luzula multiflora		0.00	0	>0.00	1	>0.00	1	0.01	1	0.00	0																				
Luzula pallescens																						0.00	0	0.00	0	0.00	0	>0.00	1	0.00	0
Lycopodium annotinum		0.00	0	0.00	0	0.00	0	0.00	0	0.01	1	10.59	32	6.82	33	4.43	27	4.40	28	6.63	33	8.39	34	7.41	35	5.61	36	6.74	37	5.41	38
Lycopodium clavatum												0.42	2	0.23	2	0.02	1	0.00	0	0.03	1										
Lysimachia thyrsiflora	WV											0.17	7	0.27	9	0.81	11	0.90	13	0.59	20	0.01	3	0.02	3	0.10	3	0.24	6	0.15	4
Maianthemum bifolium		0.00	0	>0.00	1	0.00	0	>0.00	1	0.00	0																				
Melampyrum pratense		0.05	3	0.02	5	>0.00	1	0.02	2	0.03	5	0.01	2	0.02	6	>0.00	1	>0.00	2	0.00	0	>0.00	2	0.01	3	0.05	10	0.03	6	0.01	2
Melica nutans	G	0.07	7	0.06	8	0.04	6	0.07	8	>0.00	1																				
Menyanthes trifoliata	WV											0.03	1	0.05	1	0.08	1	0.06	3	0.08	5	0.03	2	0.09	3	0.18	4	0.27	4	0.09	4
Moehringia trinervia																						0.00	0	0.00	0	0.00	0	0.00	0	>0.00	1
Molinia caerulea	G, WV	27.61	103	12.03	106	10.95	105	12.92	105	12.44	101											2.85	16	2.24	19	1.98	19	2.60	19	2.38	16
Myrica gale	WV	0.87	20	0.29	19	0.41	19	0.45	24	1.26	22	0.68	9	0.47	8	0.40	9	0.71	10	0.99	13	5.02	58	3.90	56	3.85	59	4.89	59	8.16	62
Orthilia secunda		0.01	1	0.01	1	0.01	1	0.01	1	0.01	1	0.05	3	0.03	3	0.03	3	0.06	3	0.00	0	0.00	0	>0.00	1	>0.00	2	0.01	2	>0.00	1
Parnassia palustris	RI, WV	0.04	11	0.03	8	0.05	11	0.05	13	0.04	10	0.01	2	0.01	3	>0.00	1	0.01	1	0.00	0										
Peucedanum palustre	WV	>0.00	1	0.00	0	0.00	0	0.00	0	0.00	0	0.05	5	0.03	6	0.02	6	0.02	7	0.14	16	0.01	2	0.04	2	0.03	1	0.05	2	0.01	3
Phragmites australis	G, WV	1.49	44	0.99	54	0.63	52	0.59	52	0.73	45	3.90	44	4.80	62	6.87	71	8.63	88	8.14	98	0.95	15	1.16	14	1.33	15	1.30	14	0.94	15
Picea abies	T	0.43	26	0.42	24	0.44	22	0.55	24	0.34	22	6.60	73	4.60	70	2.94	66	2.81	63	8.77	70	2.54	45	1.23	42	0.94	34	0.99	30	1.77	35
Pinguicula vulgaris	RI, WV	0.02	1	0.00	0	>0.00	1	>0.00	1	0.00	0																				
Pinus sylvestris	T	0.16	19	0.06	19	0.06	9	0.13	34	0.41	25	0.07	15	0.05	17	0.10	17	0.16	25	0.70	30	0.71	35	0.53	30	0.57	31	0.50	37	1.39	42
Poa pratensis	G											0.00	0	0.00	0	0.00	0	0.00	0	>0.00	1										
Polygala amarella	RI, WV	>0.00	1	>0.00	1	>0.00	1	>0.00	1	0.00	0																				
Potentilla erecta		2.30	77	1.55	83	1.26	80	1.60	78	1.27	72	0.13	10	0.15	10	0.18	9	0.25	10	0.22	8	0.02	3	0.03	4	0.04	4	0.04	4	0.05	4
Prunus padus	T	0.01	1	0.01	1	0.01	1	>0.00	1	0.00	0																				
Pyrola rotundifolia	WV	0.01	1	0.01	2	0.02	2	0.05	2	0.01	3																				
Rhododendron tomentosum	WV																					0.01	2	0.01	2	0.01	2	0.01	2	>0.00	1
Rubus idaeus		0.03	2	0.03	3	>0.00	1	>0.00	1	0.07	1											>0.00	1	0.00	0	0.00	0	>0.00	1	0.10	3
Rubus saxatilis		0.31	7	0.15	8	0.10	7	0.13	8	0.09	5																				
Salix caprea	T											0.00	0	>0.00	1	0.01	2	0.12	4	0.06	3										
Salix myrsinifolia	T	0.03	1	0.02	1	0.02	2	0.03	5	0.04	3	0.00	0	0.00	0	0.00	0	0.00	0	0.12	1										
Salix repens	T, WV	0.03	2	0.05	3	0.01	2	0.02	3	0.00	0											>0.00	1	>0.00	1	0.01	2	0.02	3	0.05	2
Schoenus ferrugineus	S, RI, WV	2.57	49	1.53	52	1.67	52	1.90	52	1.77	49																				
Scutellaria galericulata	WV											0.03	4	0.01	2	0.01	3	0.04	3	0.01	3	0.00	0	0.00	0	0.00	0	0.00	0	0.01	1

Species		Severmossen										Styggkärret										Ultunaviken									
	Group	2002		2003		2004		2005		2010		2002		2003		2004		2005		2010		2002		2003		2004		2005		2010	
		Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq
Selaginella selaginoides	RI, WV	0.32	28	0.21	32	0.18	28	0.19	32	0.11	24																				
Senecio sylvaticus												0.00	0	0.00	0	0.00	0	0.02	6	0.00	0										
Senecio viscosus		0.00	0	0.00	0	0.00	0	>0.00	1	0.00	0																				
Solidago virgaurea		0.03	3	0.03	4	0.02	3	0.02	4	0.00	0																				
Sorbus aucuparia	T	0.06	6	0.04	7	0.13	6	0.12	5	0.23	4	0.01	3	0.03	2	0.02	1	0.02	2	0.01	1	0.01	2	0.02	3	0.01	2	0.02	2	0.01	1
Stellaria longifolia												0.00	0	0.00	0	0.00	0	0.00	0	0.01	1										
Taraxacum vulgare		0.00	0	0.00	0	0.00	0	>0.00	1	0.00	0											>0.00	1	0.00	0	0.00	0	0.00	0	0.00	0
Trichophorum alpinum	S, RI, WV	0.03	13	0.05	17	0.06	19	0.09	19	0.10	19	0.01	1	0.01	1	>0.00	2	>0.00	2	0.00	0	>0.00	1	>0.00	1	>0.00	1	0.00	0	0.00	0
Trientalis europaea		0.16	10	0.22	15	0.16	13	0.16	14	0.02	4	0.35	36	0.22	37	0.17	28	0.24	33	0.19	34	0.09	10	0.12	21	0.08	20	0.09	21	0.03	8
Tussilago farfara		0.04	3	0.00	0	>0.00	1	0.00	0	0.00	0	0.00	0	0.00	0	>0.00	1	0.00	0	0.00	0										
Typha latifolia	WV											0.00	0	0.00	0	0.00	0	0.00	0	0.02	2										
Vaccinium myrtillus		0.00	0	0.00	0	0.00	0	0.00	0	0.01	1	0.75	18	0.52	17	0.43	18	0.55	15	0.80	18	1.53	36	1.20	38	1.17	35	1.03	34	0.94	25
Vaccinium oxycoccos	WV	0.24	18	0.28	24	0.29	21	0.32	26	0.41	32	0.51	15	0.48	16	0.49	15	0.84	21	0.94	24	4.80	78	4.79	81	4.32	83	4.26	85	4.93	86
Vaccinium uliginosum	WV	0.16	3	0.17	3	0.14	3	0.14	2	0.12	2	0.08	2	0.12	2	0.12	3	0.10	3	0.20	3	1.29	18	1.18	18	1.07	20	1.30	24	2.51	27
Vaccinium vitis-idaea		0.54	29	0.46	26	0.53	27	0.59	27	0.21	24	1.55	40	1.01	39	1.18	39	1.49	37	2.35	38	4.63	93	3.46	91	2.77	91	3.10	89	2.27	67
Viburnum opulus	T	0.00	0	0.00	0	0.00	0	>0.00	1	0.01	1																				
Vicia cracca		0.00	0	0.00	0	>0.00	1	0.00	0	0.00	0																				
Viola canina ssp. *montana*		0.03	2	0.01	2	0.01	2	>0.00	1	0.00	1																				
Viola epipsila	WV											0.03	1	0.02	1	>0.00	1	0.00	0	0.00	0										
Viola palustris	WV											0.62	22	0.54	22	0.42	25	0.69	27	0.95	35	0.27	8	0.24	10	0.16	8	0.12	9	0.19	5
Viola riviniana		0.01	1	0.01	2	0.01	2	0.01	2	0.00	0																				
Bryophytes																															
Aneura pinguis	RI, WB	0.00	0	0.00	0	0.00	0	0.00	0	>0.00	1	0.00	0	0.00	0	>0.00	2	0.01	3	0.01	3	>0.00	1	0.01	1	0.01	1	0.01	3	>0.00	1
Aulacomnium androgynum	WB											0.05	2	0.03	6	0.01	3	0.01	2	0.00	0										
Aulacomnium palustre	WB	0.00	0	>0.00	1	0.00	0	0.00	0	0.00	0	0.29	18	0.35	16	0.40	22	0.48	24	0.39	29	0.11	21	0.13	29	0.13	31	0.16	31	0.18	29
Brachytheciastrum velutinum		0.00	0	0.00	0	0.01	2	0.02	2	0.00	0	0.00	0	0.00	0	0.00	0	0.01	2	>0.00	2	0.00	0	>0.00	1	>0.00	1	>0.00	1	0.00	0
Brachythecium albicans																						0.00	0	0.00	0	0.00	0	0.00	0	>0.00	1
Brachythecium oedipodium		0.09	15	0.09	15	0.10	26	0.14	26	0.04	9	0.33	24	0.11	21	0.15	33	0.15	32	0.23	37	0.03	9	0.03	13	0.07	17	0.17	24	0.22	18
Brachythecium reflexum		0.01	3	>0.00	1	0.00	0	0.00	0	0.00	0	>0.00	1	0.00	0	0.01	3	>0.00	1	>0.00	1	0.00	0	0.00	0	>0.00	1	0.00	0	0.00	0
Brachythecium rutabulum																						0.00	0	>0.00	1	>0.00	1	0.01	1	0.01	1
Brachythecium salebrosum		>0.00	1	0.05	3	0.05	5	0.07	7	0.02	5	0.48	3	0.04	4	0.05	4	0.06	5	0.13	7	0.03	5	0.08	5	0.08	5	0.04	5	0.15	7
Bryum pseudotriquetrum	RI, WB	0.21	27	0.38	49	0.33	52	0.40	54	0.44	37	0.00	0	0.02	1	0.01	1	0.01	1	0.02	8	0.00	0	0.00	0	0.00	0	>0.00	1	0.04	4
Calliergon cordifolium	WB											0.38	5	0.45	5	0.32	6	0.24	7	0.31	14	>0.00	1	>0.00	1	>0.00	1	>0.00	1	0.01	4
Calliergonella cuspidata	WB	0.01	2	>0.00	2	0.01	2	0.01	2	>0.00	2	0.05	2	0.06	2	0.15	2	0.13	2	0.09	3										
Campyliadelphus elodes	RI, WB	0.00	0	0.03	1	0.04	2	0.03	1	0.02	1																				
Campylium protensum	WB	>0.00	1	0.01	3	>0.00	2	>0.00	1	0.00	0																				

Species		Severmossen										Styggkärret										Ultunaviken									
	Group	2002		2003		2004		2005		2010		2002		2003		2004		2005		2010		2002		2003		2004		2005		2010	
		Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq
Campylium stellatum	RI, WB	1.75	55	1.54	67	1.82	66	2.23	68	1.40	56																				
Cephalozia cf. *bicuspidata*		0.00	0	>0.00	2	0.01	4	0.02	6	0.00	0	0.03	6	0.02	3	0.05	13	0.05	15	>0.00	2	>0.00	1	0.01	3	0.02	10	0.02	10	0.01	3
Cephalozia connivens	WB	0.01	2	0.01	2	0.00	1	0.00	1	0.01	3																				
Cephalozia pleniceps	WB	0.01	1	0.00	1	0.00	2	0.01	2	0.00	0																				
Cephalozia sp.												>0.00	1	>0.00	1	0.00	0	0.00	0	0.00	0										
Cephaloziella sp.												>0.00	1	0.00	0	>0.00	1	>0.00	2	>0.00	1	0.00	0	0.00	0	>0.00	1	>0.00	1	0.00	0
Ceratodon purpureus		>0.00	1	0.00	0	0.00	0	>0.00	1	0.00	0																				
Chiloscyphus pallescens	WB											>0.00	1	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.01	2	0.01	2	0.01	1	>0.00	1
Chiloscyphus polyanthós	WB											0.00	0	0.00	0	0.00	0	0.00	0	>0.00	1										
Cinclidium stygium	RI, WB	>0.00	2	>0.00	2	0.01	2	0.01	4	0.02	7	>0.00	1	0.00	0	>0.00	2	>0.00	1	>0.00	1										
Climacium dendroides	WB											0.01	2	>0.00	2	>0.00	1	>0.00	1	0.02	2										
Dicranella heteromalla												0.01	1	>0.00	1	>0.00	1	>0.00	1	0.01	1										
Dicranella sp.		>0.00	1	0.00	0	0.00	0	0.00	0	0.00	0																				
Dicranum bonjeanii	RI, WB	0.00	0	0.00	0	>0.00	2	0.01	2	0.00	0	0.02	2	>0.00	1	0.00	0	0.00	0	0.00	0	>0.00	1	>0.00	1	0.00	0	0.00	0	0.00	0
Dicranum fuscescens/flexicaule		0.00	0	>0.00	2	0.01	3	>0.00	1	0.00	0	0.02	1	0.01	1	0.01	1	>0.00	1	>0.00	1										
Dicranum majus												0.14	3	0.12	1	0.12	1	0.12	1	0.02	1										
Dicranum montanum		>0.00	1	0.00	0	>0.00	1	0.01	3	0.00	0											>0.00	1	>0.00	1	>0.00	1	0.00	0	0.00	0
Dicranum polysetum		0.08	5	0.05	6	0.06	7	0.05	7	0.11	5	0.42	19	0.31	21	0.21	23	0.20	20	0.29	9	0.76	25	0.70	31	0.50	30	0.72	30	0.64	18
Dicranum scoparium		0.10	19	0.07	18	0.08	24	0.10	32	0.20	18	0.18	21	0.12	23	0.14	30	0.13	28	0.06	12	0.21	16	0.25	18	0.25	19	0.28	19	0.11	13
Dicranum undulatum	WB	0.00	0	0.00	0	0.00	0	>0.00	1	0.00	0																				
Drepanocladus polygamus	WB	>0.00	1	0.01	4	0.01	4	>0.00	2	0.00	0	0.03	9	0.05	13	0.06	12	0.10	15	0.16	37	0.00	0	0.01	3	0.02	7	0.01	8	0.08	8
Fissidens adianthoides	RI, WB	0.32	40	0.49	53	0.43	60	0.51	62	0.31	40																				
Fissidens osmundoides	WB	0.05	7	0.04	8	0.04	12	0.08	21	0.06	6																				
Helodium blandowii	RI, WB																					0.00	0	>0.00	1	>0.00	1	>0.00	1	>0.00	1
Herzogiella seligeri												>0.00	1	0.00	0	0.00	0	0.00	0	0.00	0										
Hylocomium splendens		0.28	7	0.17	9	0.15	10	0.18	12	0.13	10	1.04	25	0.49	25	0.39	26	0.55	21	0.31	16	0.16	12	0.12	16	0.13	15	0.13	13	0.17	9
Hypnum cupressiforme		>0.00	2	>0.00	1	0.01	1	0.01	1	0.00	0	0.00	0	0.00	0	0.00	0	>0.00	1	0.00	0										
Kindbergia praelonga																						0.01	3	>0.00	2	0.01	1	>0.00	1	0.00	0
Lepidozia reptans												>0.00	1	0.00	0	>0.00	2	>0.00	1	0.00	0										
Lophocolea heterophylla		0.14	12	0.11	16	0.11	20	0.11	28	0.04	12	0.26	38	0.14	35	0.18	37	0.31	42	0.54	39	0.04	15	0.08	26	0.10	35	0.12	33	0.17	24
Mnium hornum	WB											0.00	0	0.00	0	>0.00	1	0.00	0	0.00	0										
Onchophorus virens	RI, WB											0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	>0.00	1
Pellia cf. *epiphylla*	WB											>0.00	2	>0.00	2	>0.00	2	0.01	3	0.00	0	0.00	0	>0.00	1	0.00	0	0.00	0	0.00	0
Plagiomnium elatum	RI, WB	>0.00	1	0.01	1	0.01	3	0.01	2	0.01	3																				
Plagiomnium ellipticum	RI, WB																					0.00	0	0.00	0	0.00	0	0.00	0	0.02	1
Plagiothecium curvifolium		0.35	32	0.46	39	0.37	37	0.32	36	0.28	19	0.26	45	0.13	25	0.20	34	0.18	39	0.26	43	0.07	13	0.10	18	0.13	31	0.13	24	0.21	22
Plagiothecium denticulatum var. *undulatum*	WB																					0.10	4	0.09	5	0.05	5	0.14	5	0.09	2

Species		Severmossen										Styggkärret										Ultunaviken									
	Group	2002		2003		2004		2005		2010		2002		2003		2004		2005		2010		2002		2003		2004		2005		2010	
		Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq
Pleurozium schreberi		0.17	18	0.15	21	0.15	19	0.16	24	0.05	15	1.04	48	0.49	43	0.46	48	0.54	46	0.32	35	0.68	37	0.60	46	0.46	52	0.52	45	0.52	33
Pohlia cf. *nutans*		0.01	4	0.01	3	0.01	6	0.02	10	0.01	2	0.11	25	0.08	26	0.11	35	0.50	40	0.08	26	0.01	7	0.04	20	0.06	28	0.07	37	0.06	12
Polytrichastrum formosum												0.09	3	0.05	3	0.06	3	0.09	4	0.01	3	0.10	3	0.07	4	0.07	5	0.05	5	>0.00	1
Polytrichastrum longisetum	WB	0.06	1	0.02	1	0.03	2	0.03	2	0.03	1	0.95	31	0.77	27	0.90	40	1.95	43	1.32	30	0.19	18	0.23	24	0.26	25	0.23	26	0.07	10
Polytrichum commune	WB											9.12	50	5.81	51	8.32	53	12.41	54	11.77	60	7.02	50	6.78	53	6.24	51	8.34	54	6.66	51
Polytrichum juniperinum		0.01	3	0.01	3	0.01	3	0.01	4	>0.00	1	0.07	8	0.03	8	0.03	7	0.22	6	0.24	4	0.11	9	0.13	11	0.13	13	0.11	12	0.11	5
Polytrichum strictum	WB	0.03	1	0.03	1	0.03	1	0.03	1	0.00	0	0.31	9	0.20	9	0.20	13	0.36	17	0.99	21	1.66	47	1.72	50	1.49	52	1.21	51	2.04	42
Preissia quadrata	RI, WB	0.08	7	0.05	7	0.08	8	0.12	8	0.03	5																				
Ptilidium pulcherrimum		0.01	2	0.01	2	>0.00	1	>0.00	1	0.00	0	0.01	1	0.00	0	>0.00	2	>0.00	1	0.00	0	0.00	0	>0.00	1	>0.00	1	>0.00	1	0.00	0
Rhizomnium pseudopunctatum	RI, WB											0.03	3	0.01	2	0.03	3	0.04	5	0.05	3										
Rhizomnium punctatum	WB	>0.00	1	>0.00	2	>0.00	2	0.01	3	0.00	0																				
Rhodobryum roseum												>0.00	1	0.00	0	0.00	0	0.00	0	0.00	0										
Rhytidiadelphus squarrosus												0.00	0	0.00	0	0.00	0	0.00	0	>0.00	1	0.01	2	0.01	2	0.01	2	0.01	2	0.01	2
Riccardia cf. *latifrons*	WB											0.01	3	0.00	1	0.01	6	0.01	5	0.01	4	0.00	0	0.00	1	0.01	3	0.01	2	0.00	1
Sanionia uncinata		0.00	0	0.00	0	>0.00	1	0.00	0	>0.00	1	0.04	5	0.04	5	0.04	3	0.06	5	0.02	3	0.01	3	0.01	6	0.01	7	0.01	5	0.01	3
Scapania irrigua	WB											0.01	1	0.01	1	0.01	3	>0.00	2	>0.00	1										
Scapania paludicola	WB											>0.00	1	0.01	3	0.01	3	0.01	3	0.01	3	0.00	0	0.00	0	0.00	0	0.00	0	>0.00	1
Scorpidium cossonii	RI, WB	0.11	19	0.16	23	0.11	20	0.11	24	0.16	12																				
Scorpidium scorpioides	RI, WB	0.02	5	0.04	5	0.03	8	0.03	10	0.04	7																				
Sphagnum angustifolium	SP, WB											0.16	6	0.19	8	0.14	10	0.24	10	0.68	12	1.68	16	1.90	21	2.13	21	2.06	24	1.89	20
Sphagnum capillifolium	SP, WB											2.14	15	2.34	16	2.41	15	2.32	16	3.01	20	3.25	27	3.33	31	3.31	33	2.78	33	2.45	29
Sphagnum centrale	SP, WB											6.62	44	8.48	46	10.19	49	11.04	51	17.12	64	10.41	60	12.04	63	12.81	66	13.49	65	12.46	65
Sphagnum compactum	SP, WB											0.07	1	0.05	1	0.10	1	0.12	1	0.01	1										
Sphagnum fallax	SP, WB											0.03	4	0.05	4	0.16	4	0.14	7	0.45	12	0.48	19	0.48	19	0.56	18	0.94	17	0.90	16
Sphagnum fimbriatum	SP, WB											0.61	10	0.60	11	0.59	12	0.56	12	1.97	25	0.10	5	0.08	5	0.10	6	0.10	8	0.16	6
Sphagnum flexuosum	SP, WB											0.27	2	0.28	2	0.33	2	0.29	2	0.45	3	0.04	3	0.04	2	0.05	2	0.04	2	0.03	3
Sphagnum fuscum	SP, WB											0.32	4	0.38	4	0.32	3	0.38	6	1.00	6	2.03	27	2.51	30	2.45	32	2.76	36	3.15	27
Sphagnum girgensohnii	SP, WB											0.38	2	0.74	2	0.71	3	0.45	2	0.61	3	0.00	0	>0.00	2	0.01	2	0.02	2	0.23	2
Sphagnum magellanicum	SP, WB											0.89	5	1.16	7	1.11	6	1.28	7	1.71	6	3.19	27	3.34	28	3.57	28	4.00	29	5.39	26
Sphagnum palustre	SP, WB																					0.00	0	0.01	1	0.01	1	0.02	1	>0.00	1
Sphagnum papillosum	SP, WB																					1.01	8	1.12	8	1.22	8	1.37	8	0.85	9
Sphagnum riparium	SP, WB											0.03	1	0.06	1	0.05	1	0.07	1	>0.00	1										
Sphagnum rubellum	SP, WB																					0.02	1	0.02	1	0.03	1	0.03	1	0.03	1
Sphagnum russowii	SP, WB											2.61	14	2.84	19	2.91	26	3.03	24	3.08	35	4.80	34	5.46	37	5.41	39	5.66	40	4.68	41
Sphagnum squarrosum	SP, WB											0.36	7	0.67	9	0.21	12	0.52	15	1.81	22	0.05	3	0.05	3	0.03	4	0.05	4	0.01	2
Sphagnum subfulvum	SP, WB											0.00	0	0.00	0	0.01	1	0.03	1	0.00	0	2.96	29	3.29	35	3.26	37	3.39	38	2.84	31
Sphagnum subnitens	SP, WB											0.66	9	0.92	10	0.65	11	0.40	17	0.66	17	1.63	18	1.50	22	1.69	24	1.62	25	1.40	18

Species		Severmossen										Styggkärret										Ultunaviken									
	Group	2002		2003		2004		2005		2010		2002		2003		2004		2005		2010		2002		2003		2004		2005		2010	
		Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq	Cover	Frq
Sphagnum subsecundum	SP, WB											0.03	1	0.04	1	0.06	1	0.03	1	0.03	3										
Sphagnum teres	SP, WB											0.04	4	0.09	4	0.14	7	0.20	7	0.70	7										
Sphagnum warnstorfii	SP, WB											0.23	3	0.50	3	0.38	4	0.36	4	0.16	4	0.33	6	0.36	6	0.31	6	0.17	8	0.04	5
Sphagnum wulfianum	SP, WB											>0.00	1	>0.00	1	>0.00	1	>0.00	1	>0.00	1										
Splachnum ampullaceum	WB											>0.00	1	0.00	0	0.00	0	0.01	1	0.00	0	0.01	1	0.00	0	0.00	0	0.00	0	0.00	0
Straminergon stramineum	WB	0.00	0	0.00	0	0.00	0	0.00	0	>0.00	1	0.05	13	0.08	14	0.05	19	0.06	18	0.19	23	0.09	14	0.08	15	0.06	17	0.08	13	0.13	16
Warnstorfia exannulata	WB																					0.00	0	0.00	0	>0.00	1	>0.00	1	0.00	0
Plant litter		91.08		93.08		87.73		81.38		78.32		58.24		63.26		39.04		35.35		37.12		47.10		47.54		45.13		40.58		48.04	
Bare peat		0.45		7.76		7.06		12.02		4.84		0.03		1.36		24.60		25.27		0.98		0.73		0.03		3.56		14.24		0.91	
Bryophytes		3.90		4.00		4.13		4.83		3.41		31.29		29.43		33.15		40.48		51.33		43.39		46.84		47.26		51.06		48.23	
Vascular plants		41.77		22.01		20.82		24.93		24.90		31.29		27.28		32.39		43.81		54.14		40.40		38.36		37.21		43.79		44.11	
Sedges (rich fen indicators included)		2.91		2.39		2.79		3.45		2.65		1.66		2.53		6.13		12.69		8.59		4.10		6.96		8.70		10.74		7.65	
Sedges (rich fen indicators excluded)		0.28		0.77		1.02		1.32		0.75		1.65		2.51		6.13		12.56		8.53		4.09		6.96		8.70		10.74		7.65	
Grasses		30.63		13.89		12.47		14.61		13.83		5.71		7.37		10.71		13.56		14.80		5.65		5.63		5.52		6.74		3.96	
Rich fen indicators, vascular plants		3.16		1.93		2.09		2.48		2.16		0.02		0.02		0.01		0.14		0.06											
Rich fen indicators, bryophytes		2.49		2.70		2.87		3.46		2.43		0.05		0.03		0.05		0.07		0.08		0.00		0.01		0.01		0.01		0.06	
Sphagnum												15.45		19.39		20.46		21.45		33.45		31.99		35.53		36.94		38.48		36.51	
Wetland vascular plants		35.76		17.73		16.87		20.19		21.02		10.48		13.48		22.82		33.51		34.23		22.35		24.27		25.92		31.21		32.06	
Wetland bryophytes		2.67		2.82		3.01		3.64		2.54		26.88		27.32		31.05		37.79		48.87		41.18		44.63		45.28		48.75		45.90	
Juvenile trees		1.50		1.01		1.22		1.91		3.97		7.40		5.88		5.64		6.30		15.61		3.48		2.32		2.49		3.04		6.00	

CHAPTER III

A functional trait approach to fen restoration analysis

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A functional trait approach to fen restoration analysis

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Keywords
Bryophyte; Ditch blocking; Environmental filter; Functional diversity; Peatland; Specific leaf area; Tree cutting; Vascular plant

Nomenclature
Mossberg & Stenberg (2003) for vascular plants; Hallingbäck et al. (2006) for bryophytes

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Abstract

Questions: Ecological restoration has traditionally been evaluated with analyses focused on species identities and abundances. These analyses provide no ecological explanation to why certain species change in abundance. One solution may be a functional trait analysis. We asked whether shifts in functional traits could explain vegetation changes in fens restored through tree cutting and rewetting, and how the functional traits in the restored sites compare to those of the reference site?

Location: Three former rich fens in east-central Sweden.

Methods: Tree cutting and rewetting were applied in a factorial design, and species and abundance data were recorded for 8 yrs. Abundance data and trait data of canopy height, specific leaf area (SLA) and diaspore mass were used to calculate functional richness (FRic), functional divergence (FDiv), functional dispersion (FDis) and community-weighted mean (CWM) of functional traits. Data were analysed in a linear mixed effect model for vascular plants and bryophytes jointly, and for vascular plants separately. Results of restoration treatments were compared to data from a reference site.

Results: Among vascular plants, tree cutting caused a decrease in SLA, as shade-sensitive species increased. In accordance with the change in SLA, FDis increased. In the joint analysis, tree cutting led to increased FDis, FDiv and FRic, indicating reduced filtering caused by the removal of the shading canopy, which allowed shade-sensitive species to establish. The comparison to the reference site shows that even after 8 yrs, the restoration treatments have higher trait diversity than the reference site, indicating that the restoration sites have a too relaxed trait filter compared to conditions in an undisturbed fen. Our interpretation is that this is primarily caused by insufficient rewetting (and increased nutrient availability) that allow species of both natural and degraded fen conditions to co-exist, and which failed to suppress the regrowth of trees.

Conclusions: Analysis of functional diversity improves our understanding of the ecological mechanisms affecting restoration results, and allows comparison among regions and communities with different species composition.

Introduction

During the last decades, restoration of degraded ecosystems has been conducted in an attempt to restore biological diversity and ecosystem functions in a wide range of communities. The end result has usually been a system somewhere between the degraded system and the reference site (e.g. Moreno-Mateos et al. 2012). Success has often been measured in terms of number of target species, or diversity indices that combine species number and the relative abundance of each species (e.g. Shannon–Wiener index or Simpson's diversity index; Shannon 1948; Simpson 1949). Although these parameters have the advantage of being simple to measure, they do not provide information regarding the diversity of functions present, and hence provide no information on the processes and mechanisms that control species recruitment and succession in restored communities. Further, the responses of individual species are of limited value outside their range of distribution.

Recently, functional diversity indices have been introduced to community ecology as metrics that take into account species ecological functions (Mason et al. 2005), and therefore help to measure how human impacts affect various aspects of ecosystem function (Laliberté et al.

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2010; Bernhardt-Römermann et al. 2011). Functional diversity indices have so far been rarely used to evaluate the outcome of ecological restorations (Hedberg & Kotowski 2010; Cadotte et al. 2011). They could be powerful tools for analysing mechanisms of species pool filtering during community reassembly in restoration projects (Funk et al. 2008), and thus for identifying ecological constraints of restoration projects.

Evaluating the importance of abiotic, biotic and dispersal filters is central to understanding processes operating during ecological restoration (Funk et al. 2008). This is particularly the case for restoration of wetland communities, which are jointly controlled by soil anoxia (a strong habitat filter), pH and inter-specific competition (Kotowski & van Diggelen 2004; Kotowski et al. 2006). In addition, many fen species have poor dispersal ability, which may limit the restoration of fen communities (e.g. Middleton et al. 2006; Rasran et al. 2007).

A typical feature of peatland vegetation is the co-dominance of vascular plants and bryophytes. This complicates functional analyses, because functional traits have rarely been quantified for bryophytes. In addition, ecological and morphological differences between bryophytes and vascular plants make it difficult to combine them in one analysis. Some functional traits can only be measured for one of the groups (e.g. root traits), and even traits that are common to both groups differ in function, which prevents comparisons. Nevertheless, excluding bryophytes is unacceptable in ecosystems where they are important for ecosystem functions. For example, peat mosses (*Sphagnum* spp.) are the main drivers of succession from rich fen to bog communities (Rydin et al. 2006; Granath et al. 2010), which over time reduce vascular plant access to groundwater and minerals.

In the present study we apply a functional diversity analysis to the outcomes of a previously reported restoration experiment of three peatlands drained for forestry, in which rewetting and tree cutting were conducted to restore openness and hydrology (Hedberg et al. 2012). Both rewetting and tree cutting increased the cover of *Sphagnum*, wetland bryophytes and sedges. Tree cutting increased the cover of grasses, wetland vascular plants and juvenile trees. Both treatments resulted in increased species numbers, and a combination of them was most effective, but the target rich fen specialists still did not recover (Hedberg et al. 2012). In this study, we focus on how functional traits of vascular plants and bryophytes respond to restoration treatments to shed light on mechanisms that determine or limit restoration success. We analyse functional traits in the leaf–height–seed (LHS) strategy scheme (specific leaf area, canopy height and diaspore mass) proposed by Westoby (1998). Specific leaf area (SLA) is particularly relevant for the shade tolerance of species (Jansen Klooster et al. 2007) as well as for their response to disturbance. Canopy height determines the ability to compete for light (Kotowski & van Diggelen 2004). Diaspore mass is important for seed bank persistence, dispersal ability (Greene & Johnson 1993) and germination success (Bruun & Ten Brink 2008).

We analyse the community-weighted mean (CWM; e.g. Garnier et al. 2004, 2007) of the traits, as well as the functional diversity indices, functional richness (FRic), functional divergence (FDiv; Mason et al. 2005; Villéger et al. 2008) and functional dispersion (FDis; Laliberté et al. 2010) in relation to the restoration measures.

Our main hypothesis is that tree cutting relaxes the abiotic filter 'shading', which should be reflected by a decrease in mean SLA and an increase in functional diversity, because shade-tolerant and shade-sensitive species may be able to co-exist. However, the establishment of new species may be constrained by dispersal ability, so that species with small diaspores would be the first to colonize the restored plots or may still be present in the seed bank. This should be reflected by a decrease in mean diaspore mass. Furthermore, reduced shading by trees may increase competition for light among understorey species, which should be reflected by an increase in mean canopy height. Rewetting is expected to intensify the abiotic filter of anoxia, which should be reflected by a decrease in functional diversity. Finally, our previous conclusion, that restoration through the combination of tree cutting and rewetting was most successful (Hedberg et al. 2012), should be reflected in functional diversity indices that are closest to those of an undisturbed reference site.

Methods

Restoration measures and experimental design

In this study, three fens (Severmossen, Styggkärret and Ultunaviken) in the province of Uppland, east-central Sweden, were restored through tree cutting and ditch blocking. The species composition prior to restoration was characteristic of a drained and tree-encroached fen, with the five most abundant species being *Molinia caerulea*, *Lycopodium annotinum*, *Sphagnum centrale*, *Polytrichum commune* and *Picea abies*. Data from 1979 from a rich fen site in Gästrikland (east-central Sweden, 60°51′N, 17°10′E) that at the time had not yet been affected by drainage were included as a reference site (Mälson et al. 2008). This site was drained in 1980, but prior to drainage the five most abundant species were *Carex rostrata*, *Scorpidium scorpioides*, *Myrica gale*, *Campylium stellatum* and *Carex livida*, which resembles the pre-drainage conditions at Styggkärret and Ultunaviken (von Krusenstjerna 1945; Almquist 1965). Mean temperature at the nearby meteorological station in

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Uppsala is −4.2 °C in January and 16.4 °C for July; annual precipitation is 544 mm (SMHI 2005).

The three sites were drained for forestry purposes in the 1950s and were then rapidly colonized by *Betula pubescens*, *Pinus sylvestris* and *Picea abies*. Between Dec 2002 and Jun 2003 all three sites underwent restoration in the form of rewetting (by ditch blocking) and tree cutting. The rewetting was done by placing three dams in the upper 150 m of the ditch, with 50 m distance between the dams, with the last dam in the middle of the restoration site. Tree cutting was done on one side of the ditch (300 m × 50 m). This resulted in four field plots (50 m × 150 m) per site representing a factorial combination of rewetting (RW: rewetted vs drained) and tree cutting (TC: tree cut vs forest). In this study, the term 'treatment combination' is always used when a combined treatment is referred to (e.g. the tree cut and rewetted treatment combination). Four transects were placed perpendicular to the ditch in each treatment combination with 30 m between transects. A permanent plot (50 cm × 50 cm) was placed along the transects at 4, 8, 16, 24 and 32 m from the ditch. The rewetted and cut treatment combination had more intense sampling, with three plots per distance (Fig. 1). The plots were monitored for species cover of vascular plants and bryophytes in 2002 (year 0, pre-treatment) and in 2003–2005 (year 1–3) and 2010 (year 8). Among trees, individuals older than the restoration experiment were excluded from the analysis. For further details regarding the sites and the design, see Hedberg et al. (2012).

Indices of functional diversity

The three functional diversity indices we use measure different aspects of functional diversity (hereafter referred to as FD). Functional richness (hereafter referred to as FRic) measures the size of the filled niche space (Mason et al. 2005; Villéger et al. 2008); functional divergence (FDiv) is a measure of functional heterogeneity (Kotowski et al. 2010) that measures the divergence of abundance in the trait space (Mason et al. 2005; Villéger et al. 2008); functional dispersion (FDis) is a variance measure that describes the dispersion of species in a trait space (Laliberté & Legendre 2010). We also analyse the response of individual functional traits to the restoration treatments. This is done by calculating the community-weighted mean (CWM) of the traits, which is a measure of the dominant trait value in a community (e.g. Garnier et al. 2004, 2007; Diaz et al. 2007). In the Results and Discussion, all references to changes in trait values refer to changes in the CWMs of these traits.

For vascular plants, values for SLA were mainly taken from the LEDA Trait base (Kleyer et al. 2008). When values for a given species were missing from LEDA but data on taxonomically similar species were available, data from the latter were used to avoid missing values. If several similar species existed, a weighted average was used, with weights being the amount of samples used in LEDA for the similar species. For canopy height of vascular plants, most values were taken from LEDA, but one species had values from the Ecoflora database (Fitter & Peat 1994), and one species value was estimated from the relative height of the leaf aggregation in proportion to existing release height data. Diaspore mass data for vascular plants were mainly taken from LEDA, three values were taken from the Kew Seed Information Database (SID) v 7.1 (Royal Botanic Gardens Kew 2008), and 10 values were taken from published literature (Appendix S4). The reported average diaspore mass was used when selecting diaspore mass data from LEDA. The highest average was used when several values existed. Vascular cryptogams (e.g. *Lycopodium*) were assumed to have spherical spores with the same density as water. Diaspore mass values were then calculated by obtaining spore radius from published literature (Appendix S4).

For bryophytes, canopy height values were mainly taken from BRYOATT (Hill et al. 2007), with two values taken from the Bryophyte Flora of North America (Ireland 2007; Ignatov 2009) and one value from Atherton et al. (2010). Diaspore mass for bryophytes was calculated by assuming spherical spores, and assuming the same density as water. All data on spore diameter for bryophytes were taken from BRYOATT (Hill et al. 2007). As for vascular plants, data from taxonomically similar species, or the average of several related species, were used in a few cases when data were missing. For an exact description of each species data source, criteria used in LEDA and hierarchy order of sources, see Appendices S4 and S6.

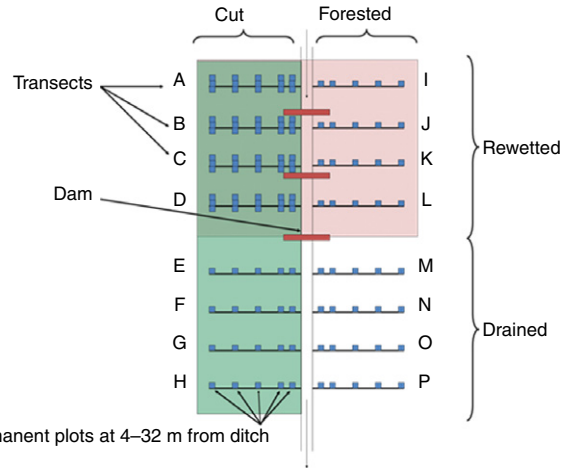

Fig. 1. Experimental design at the restoration sites [From Hedberg et al. (2012) with permission].

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Statistical analysis

The CWM, FRic, FDiv and FDis values were calculated in the package FD (Laliberté & Legendre 2010) in R (R Foundation for Statistical Computing, Vienna, AT). All traits were standardized to mean 0 and unit variance. FRic was standardized to the global FRic, which includes all species, in order to constrain it between 0 and 1. CWM, FDiv and FDis were weighted by abundance. The few plots that did not have more species than the number of traits analysed (a requirement for calculating FRic and FDiv) were removed from the analysis for that year.

The response of diversity indices over time was examined with a linear mixed effect model using the function lme in the nlme package in R. For this analysis, the experiment was treated as a split-plot design, with restoration treatments as main plot factors, site as a main plot blocking factor and time as a split-plot factor. Thus the level of replication for the test of restoration effects (RW, TC and RW × TC) was the 50 m × 150 m field plot ($N = 3$ sites × 4 plots = 12), whereas the level of replication for the effects of time, and the interaction between time and restoration effects (RW × time, TC × time and RW × TC × time), was time within field plot ($N = 5 \times 12 = 60$). In practice this was achieved by treating site, the two restoration treatments (RW and TC) and time as fixed factors, and site × TC × RW as a random factor. We used the interaction between time and restoration treatments (RW, TC or RW × TC) as an indication of the restoration treatment effects on the FD indices to ensure that potential differences in starting conditions did not influence the analysis. The restoration treatment FD indices, trait values (measured as CWM) and species number at year 8 were compared to data from the reference site with a two-sample Wilcoxon test.

Prior to the analysis, all observations were aggregated to the level of time within field plots (i.e. the split-plot level). To give an equal weight to all distances and transects, aggregation of data was done in a step-wise manner; first averaging the triplicate plots at the same distance in each transect in the 'rewetted and cut' treatment combination, then averaging over all distances along each transect, and finally averaging over all transects within each field plot.

To achieve normal distribution of residuals, variants of logarithmic and/or root transformations were required for some indices. Details on transformations are presented in Table 1a,b.

Results

In Table 1a,b we present the statistically significant effects on which the presentation and discussion are focused. All

Table 1. Response of functional diversity indices and community-weighted mean (CWM) of functional traits to tree cutting (TC), rewetting (RW), time and their interactions in the (a) joint (bryophytes and vascular plants) analysis and (b) vascular plant analysis.

(a) Source	num DF	den DF	FRic			FDiv			FDis			CH			DM		
			Tr	*F*	*P*	Tr	*F*	*P*	Tr	*F*	*P*	Tr	*F*	*P*	Tr	*F*	*P*
RW	1	6	1	1.37	0.29	0	1.4	0.28	2	0.59	0.47	0	0.04	0.84	1	0.16	0.7
TC	1	6	1	0.43	0.54	0	0.67	0.45	2	6.45	0.04	0	5.97	0.05	1	6.1	0.05
Time	4	32	1	3.68	0.01	0	0.49	0.74	2	2.93	0.04	0	1.33	0.28	1	1.36	0.27
RW × TC	1	6	1	0.37	0.57	0	0.84	0.4	2	2.00E-03	0.96	0	0.22	0.66	1	0.05	0.83
RW × Time	4	32	1	0.49	0.74	0	2.29	0.08	2	1.21	0.33	0	2.33	0.08	1	0.77	0.55
RW × TC × Time	4	32	1	1	0.42	0	0.65	0.63	2	1.08	0.38	0	0.35	0.84	1	0.25	0.91
TC × Time	4	32	1	3.63	0.02	0	4.31	0.01	2	6.29	7.00E-04	0	2.45	0.07	1	1.47	0.24

(b) Source	num DF	den DF	FRic			FDiv			FDis			CH			DM			SLA		
			Tr	*F*	*P*	Tr	*F*	*P*	Tr	*F*	*P*	Tr	*F*	*P*	Tr	*F*	*P*	Tr	*F*	*P*
RW	1	6	3	0.25	0.64	4	3.03	0.13	0	0.01	0.92	0	0.01	0.92	5	0.01	0.94	6	1.55	0.26
TC	1	6	3	0.02	0.89	4	13.98	0.01	0	0.87	0.39	0	0.06	0.81	5	1.28	0.3	6	0.59	0.47
Time	4	32	3	1.81	0.15	4	1.1	0.37	0	1.81	0.15	0	1.69	0.18	5	0.9	0.47	6	1.52	0.22
RW × TC	1	6	3	0.05	0.83	4	2.98	0.13	0	0.08	0.79	0	0.28	0.62	5	0.5	0.5	6	0.19	0.68
RW × Time	4	32	3	0.87	0.49	4	1.22	0.32	0	2.47	0.06	0	2.48	0.06	5	0.29	0.88	6	6.13	9.00E-04
RW × TC × Time	4	32	3	0.89	0.48	4	0.88	0.49	0	0.34	0.85	0	1.09	0.38	5	0.46	0.77	6	1.25	0.31
TC × Time	4	32	3	0.63	0.64	4	2.34	0.08	0	7.51	2.00E-04	0	1.61	0.2	5	0.63	0.64	6	3.76	0.01

numDF = numerator degrees of freedom, denDF = denominator degrees of freedom. FRic = Functional richness, FDiv = Functional divergence, FDis = Functional dispersion, CH = Canopy height, DM = Diaspore mass, Tr = Transformation, Tr 0 = Untransformed, Tr 1 = $\log10(x + 1)^{(1/4)}$, Tr 2 = $\log10(x + 1)^{(1/7)}$, Tr 3 = $x^{(1/7)}$, Tr 4 = $x^{(1/3)}$, Tr 5 = $x^{(1/2)}$, Tr 6 = $x^{(1/4)}$, *F* = *F*-value.

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effects but one were caused by tree cutting × time, and there were no significant tree cutting × rewetting × time interactions.

Tree cutting: joint analysis

Tree cutting had a significant effect on the development of FDis, FDiv and FRic in the joint analysis, as indicated by a significant interaction between tree cutting and time for FRic, FDiv and FDis (Table 1a). FDis changed very little for the forested treatment, also with little change in response to tree cutting during the first 3 yrs, but between year 3 and 8 FDis doubled (Fig. 2a). FDiv increased rapidly between year 1 and 3 in the tree cutting treatment, and decreased continuously in the forested treatment over the 8 yrs (Fig. 2b). FRic increased in response to tree cutting, being 2.5 times higher in year 8 than in year 0, but the increase decelerated with time (Fig. 2c). Canopy height showed a strong increasing trend in response to tree cutting between year 3 and 8, but although the *P*-value was low ($P = 0.07$), this trend was not significant.

Tree cutting: vascular plant analysis

In the separate analysis for vascular plants, tree cutting had a significant effect on FDis and SLA, as indicated by a significant interaction between tree cutting and time for FDis, and SLA (Table 1b). FDis changed very little during the first 3 yrs in the tree cut treatment, but increased by almost 60% between year 3 and 8 (Fig. 3a). SLA decreased

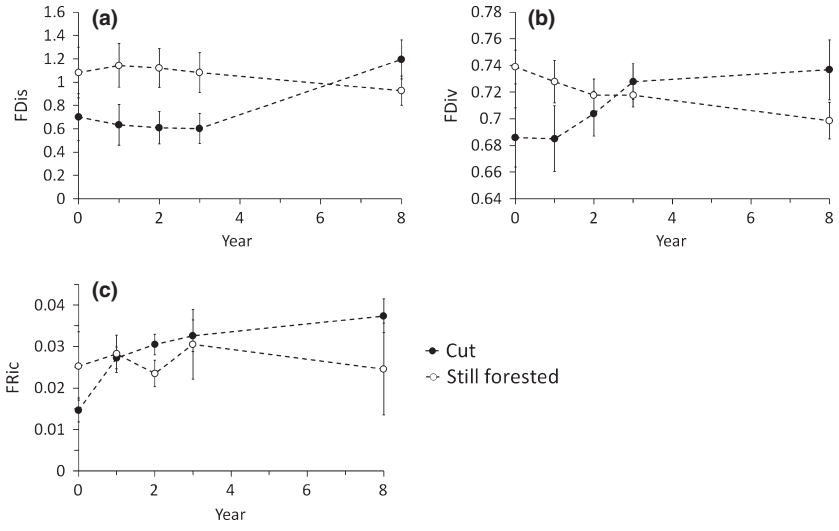

Fig. 2. The response of (**a**) Functional dispersion (FDis), (**b**) Functional divergence (FDiv), (**c**) Functional richness (FRic) to tree cutting (trees cut vs. still forested, drained and rewetted plots pooled) in the joint analysis (vascular plants and bryophytes). Error bars represent +/− one standard error.

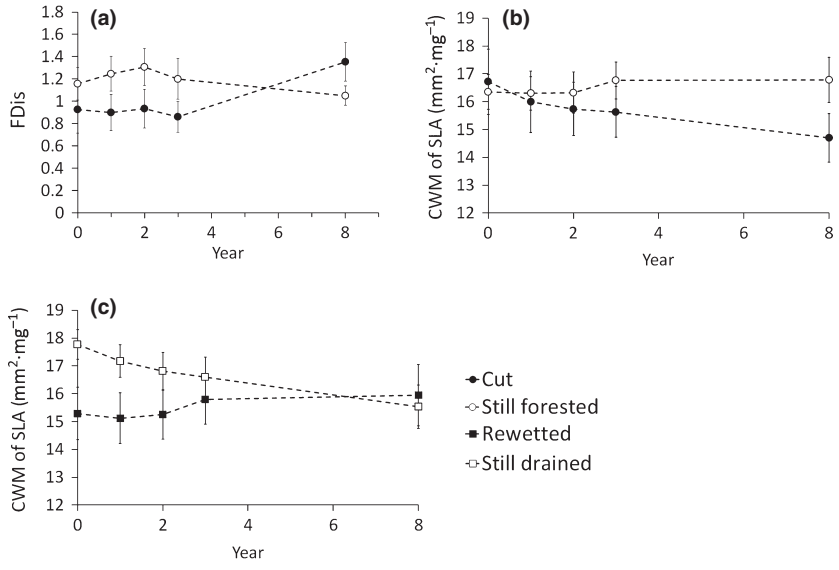

Fig. 3. The response of (**a**) Functional dispersion (FDis), (**b**) Community weighted mean (CWM) of specific leaf area (SLA) to tree cutting (trees cut vs. still forested, drained and rewetted plots pooled) in the vascular plant analysis (**c**) Community weighted mean (CWM) of specific leaf area (SLA) to rewetting (rewetted vs. still drained, tree cut and forested plots pooled) in the vascular plant analysis. Error bars represent +/− one standard error.

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continuously in the tree cut treatment, whereas it remained fairly stable in the forested treatment (Fig. 3b).

Rewetting: vascular plants

There was a marginal increase in SLA in the rewetted treatment, whereas SLA decreased significantly and continuously in the still drained treatment by a total of 14% (Table 1b, Fig. 3c). Most of the decline in the still drained treatment occurred in the cut and still drained treatment combination (data not shown).

Restoration treatments compared to the reference site

Rewetting and tree cutting showed strong differences in trait values and trait composition, as well as species richness, compared to the reference site. For the joint analysis, both tree cutting and rewetting differed significantly from the reference site in FDis, canopy height and species richness, all being significantly higher in the two restoration treatments than in the reference site (Fig. 4b–d). The tree cut treatment in the joint analysis also had a significantly higher FRic than the reference site (Fig. 4a). For the vascular plant analysis, both tree cutting and rewetting differed significantly from the reference site in FRic, FDis and canopy height, all being significantly higher in the two restoration treatments than in the reference site (Fig. 4a–c). The treatment combination with both the restoration treatments (cutting and rewetting) applied together differed significantly in FRic, FDis, CWM of canopy height and species richness in both the joint analysis and the vascular plant analysis (Fig. 4a–c). There was no indication that the treatment combination with the two restoration treatments (cutting and rewetting) applied together was more similar in FD to the reference site than any of the main treatments of cutting or rewetting.

Discussion

Trait values and functional diversity

The results reveal strong shifts in trait values and composition of the analysed traits as a consequence of the changed light and hydrological filters caused by the restoration treatments. SLA changed significantly as a result of tree cutting. The increase of FDis in response to tree cutting indicates increased total variance of trait values associated with the influx of species with low SLA.

For the joint analysis, no individual trait changed significantly, but the strong increase in FRic, FDiv and FDis in response to cutting clearly shows that the total amount of filtering was reduced when tree cutting released the vegetation from shading, allowing a more heterogeneous trait composition (higher FDiv) with higher richness (FRic) and higher variance (FDis). The decelerating strength of the

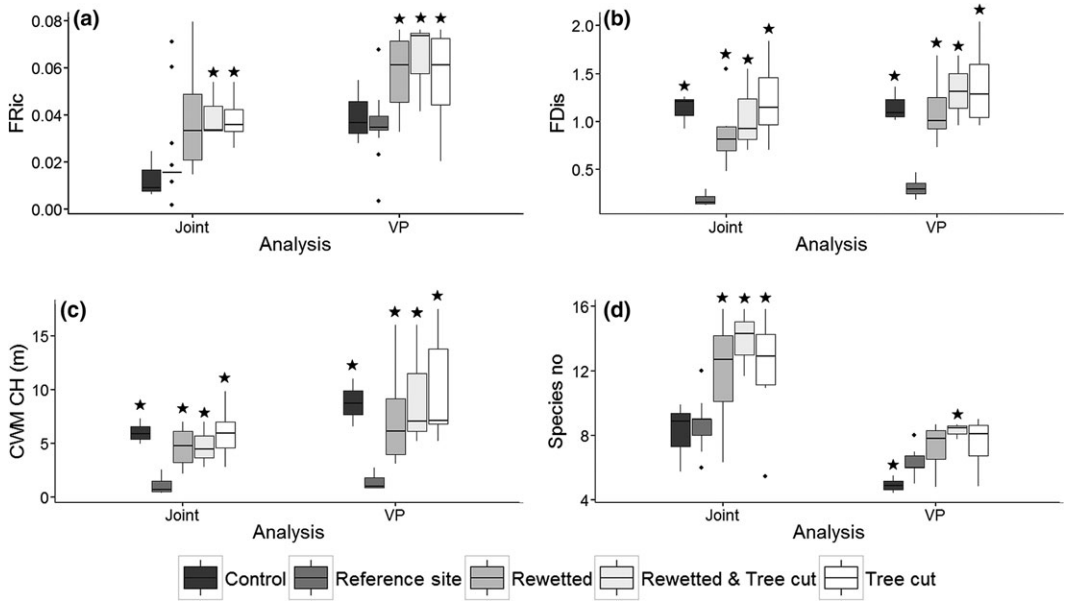

Fig. 4. Boxplots showing the distribution of (**a**) Functional richness (FRic), (**b**) Functional dispersion (FDis), (**c**) Community weighted mean of canopy height (CWM CH), (**d**) Species richness (Species number) in the rewetted and tree cut treatments, the control (still drained and with trees), and in the reference-site (eight years after cutting and rewetting) for the joint analysis (Joint) and the vascular plant-analysis (VP). Black central line shows the median value. The upper and lower hinges are the third and first quartile respectively. Notches show the lowest value outside the hinge that is within 1.5 × Inter Quartile Range. A star above the upper hinge indicates statistical difference from the reference-site.

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increase in FRic with time may be a result of competition making new species establishment less likely as the community closes.

The continuous decrease in SLA in response to tree cutting shows that species with lower investment in photosynthesis and slower return on investments increase in dominance with time (Westoby 1998). Although this is a common phenomenon in regrowth of coniferous forest (Westoby 1998), our results cannot solely be explained by an increase in conifers, since the result remained significant and graphically similar in a control analysis where trees were removed from the data set. Our interpretation of the development of SLA is that low SLA species are more shade-sensitive (Janse-ten Klooster et al. 2007) and should benefit from the removal of tree canopy, and that they are proposed to be stronger competitors in the long term in areas with low-nutrient availability (van der Werf et al. 1993). Thus, when the shading filter is removed, species with a low SLA are favoured. The increase of FDis among vascular plants in response to tree cutting indicates an increased variance of trait values due to reduced environmental filtering, which occurs as the removal of the shading canopy increases the abundance of species with a lower SLA that were previously limited by shading.

Aside from the decrease in SLA in the tree cut treatment, a similar decrease occurred in the still drained treatment. Our interpretation is that the strong decrease in the drained treatment is mostly an artefact, since it was most pronounced in the drained and cut treatment combination. A shift towards dominance of species with a low SLA, and a trend of increasing canopy height would be expected in a resprouting coniferous forest (Reich et al. 1999). In waterlogged fen habitats, one would expect anoxic conditions to reduce competition (Kotowski et al. 2010) and suppress regrowth of high-canopy species.

Comparisons with the reference site

As is often the case in ecological restoration, the restoration sites differ significantly from the reference site. It is clear that for both the joint and vascular plant analyses, canopy height is significantly higher in the restoration site, which indicates that the increase in water level has not been sufficient to suppress the regrowth of tall-growing, competitive species. It is also known that rewetting can be coupled with a nutrient release effect (cf. Turner & Haygarth 2001), and this could have contributed to the regrowth of trees. The reference site shows clear signs of strong abiotic and biotic filters that are characteristic of an undisturbed fen (Kotowski & van Diggelen 2004; Kotowski et al. 2006). This stronger filtering is evident from the significantly lower FRic and FDis in the reference site compared to both restoration treatments in the vascular plant analyses. In the joint analyses, it is evident from the significantly lower FDis in the reference site compared to both restoration treatments, and to the significantly lower FRic in the reference site, compared to the tree cut restoration treatment. These results show that the reference site has lower trait diversity, characteristic of a site with a stronger environmental filter. We can also conclude that there is no support for our hypothesis that the treatment combination of cutting and rewetting applied together is more similar in FD to the reference site than any of the main treatments (cutting or rewetting).

Literature data vs field measurements

In this study, we use trait values reported in trait databases and published literature, instead of measuring the traits directly in the field. The advantage of this method is the significant reduction in labour that would otherwise be required for field measurements of traits for species, where new species requiring measurement of traits may appear each year. This advantage, however, comes at the cost of applying trait values collected in Central Europe (as is the case in LEDA) for species growing in Scandinavia. Considering that inter-species variations in trait values dominate, particularly when the environmental gradients are strong (Auger & Shipley 2013), our conviction is that the benefits outweigh the noise associated with intra-specific trait variation.

Conclusions

We have shown how changes in functional traits during ecological restoration can be analysed through a functional trait analysis, and how the results obtained can be used to draw conclusions regarding how restoration actions affect functional traits by modifying the environmental filters. A species-based analysis can provide information on vegetation changes that occur in response to restoration measures, but it provides no general ecological explanation for the processes that drive these changes. This is the main argument for why a functional approach can benefit the field of restoration ecology. By comparing, for the system, important functional traits, from the restoration treatments to those of the reference site, information on potential reasons for failure can be gained. In our study, this relates to the higher FD in the restoration treatments, which indicates a too relaxed filter, likely caused by insufficient rewetting (Hedberg et al. 2012), which has not succeeded in creating a sufficiently strong anoxic filter that would suppress regrowth of high-canopy species.

A word of caution is warranted when evaluating restoration projects based on FD. High FD is not an automatic goal for ecological restoration: whether high FD is positive

or negative depends on the system analysed. Combined with ecological knowledge about the reference site conditions, a functional analysis can provide added insight into if and how the restoration sites differs in trait composition from the reference site. By not limiting the analyses to species identities, the results become relevant for similar ecosystems outside the geographic distribution of the analysed species, providing greater value for the science of ecological restoration.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Location of restoration sites and reference site.

Appendix S2. Expanded Fig. 4 showing all indices.

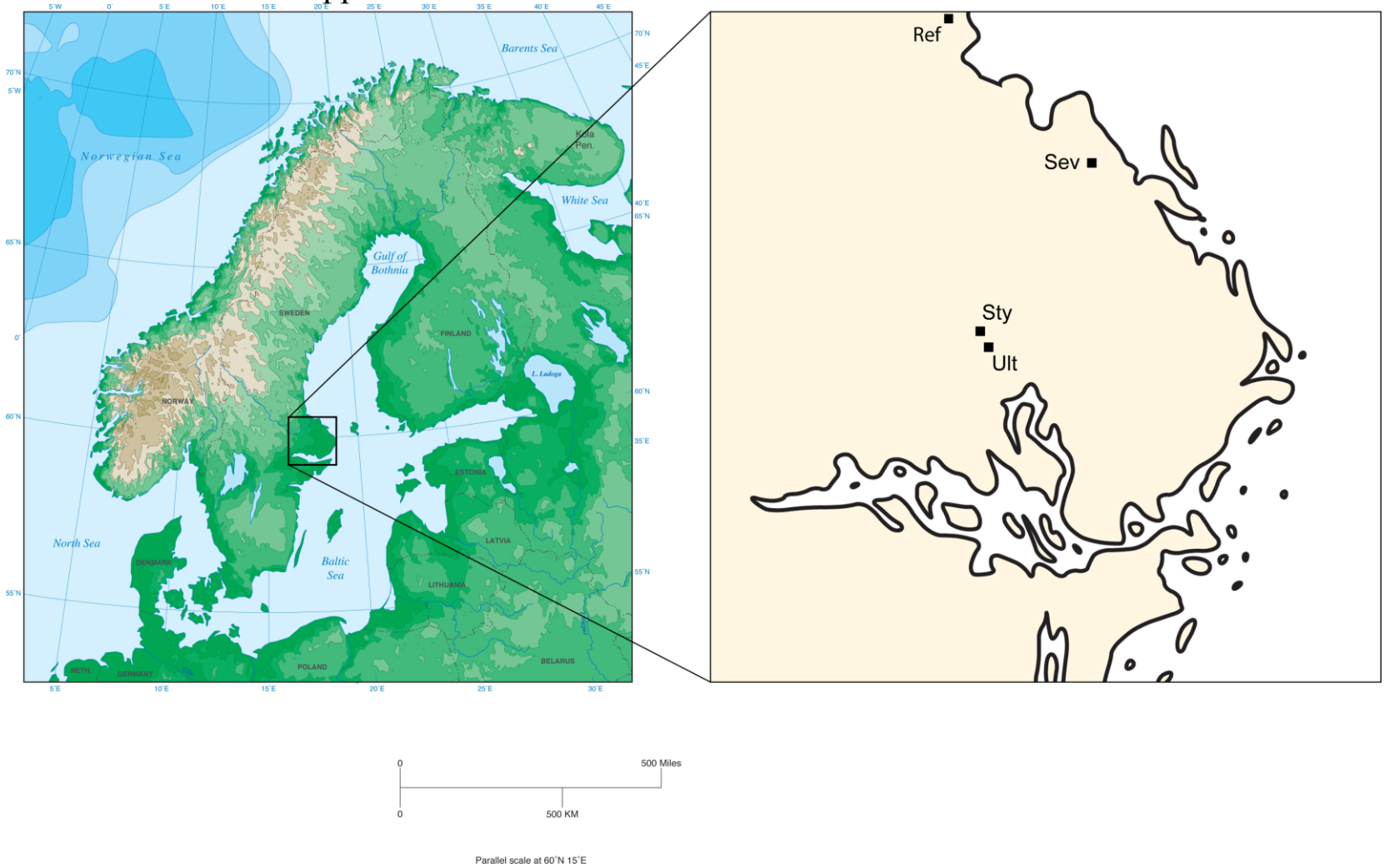
Appendix S3. Expanded Fig. 4, where the two restoration treatments are replaced by the four treatment combinations.

Appendix S4. Trait sources for species.

Appendix S5. Table showing result from the Wilcoxon two-sample test, comparing the restoration treatments with the reference site.

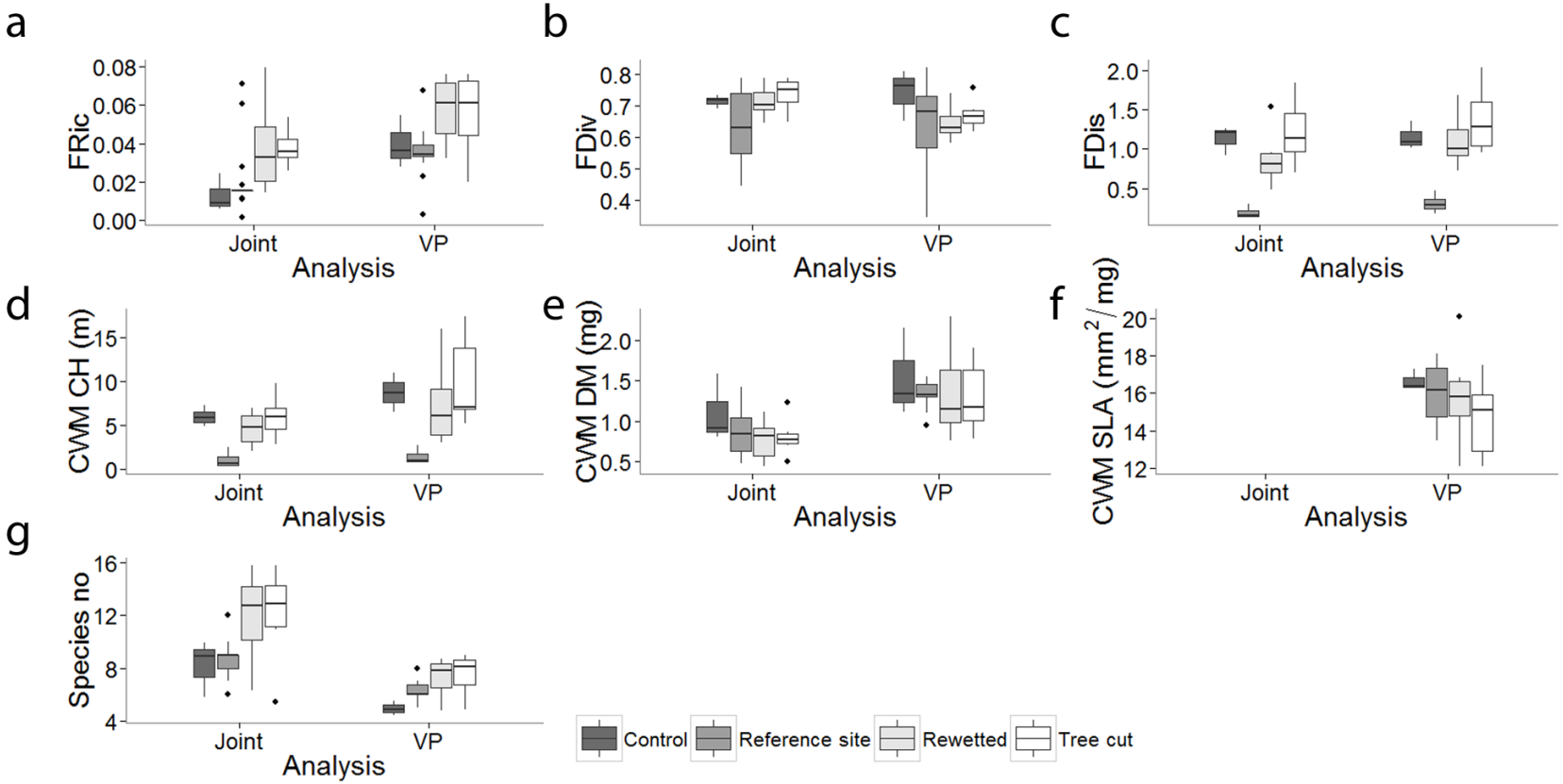
Appendix S6. Trait sources for species, criteria used in LEDA and hierarchies of sources.

Appendix S1: Location of restoration sites and reference site



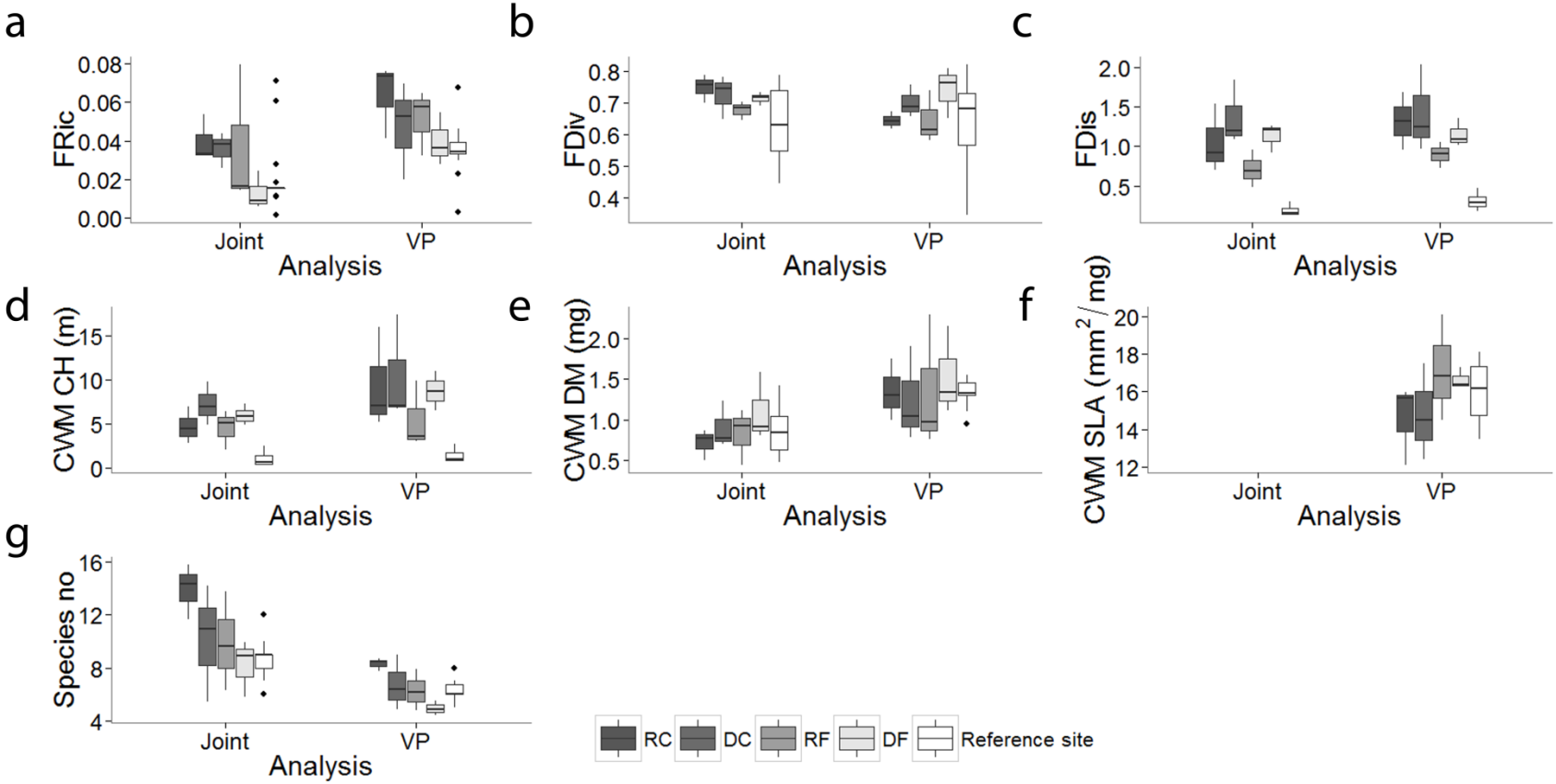
Location of the restoration sites and the reference site in central eastern Sweden (Modified from Hedberg et al. (2012) with permission).

Appendix S2:Expanded Fig 4 showing all indices



1:2 Boxplots showing the distribution of a: Functional richness (FRic), b: Functional divergence (FDiv), c: Functional dispersion (FDis), d: Community weighted mean of canopy height (CWM CH), e: Community weighted mean of diaspore mass (CWM DM), f: Community weighted mean of specific leaf area (CWM SLA), g: Species richness (Species no) at year 8 in the two restoration treatments and the reference site and control for the joint analysis (Joint) and the vascular plant analysis (VP). Black central line shows the median value. The upper and lower hinges are the third and first quartile respectively. Notches show the lowest value outside the hinge that is within 1.5 × Inter Quartile Range.

Appendix S3: Expanded fig 4 where the two restoration treatments are replaced by the four treatment combinations



1:3 Boxplots showing the distribution of a: Functional richness (FRic), b: Functional divergence (FDiv), c: Functional dispersion (FDis), d: Community weighted mean of canopy height (CWM CH), e: Community weighted mean of diaspore mass (CWM DM), f: Community weighted mean of specific leaf area (CWM SLA), g: Species richness (Species no) at year 8 in the four treatment combinations rewetted & cut (RC), drained & cut (DC), rewetted & forested (RF), drained & forested (DF), as well as within the reference site. The analysis is shown for the joint analysis (Joint) and the vascular plant analysis (VP). Black central line shows the median value. The upper and lower hinges are the third and first quartile respectively. Notches show the lowest value outside the hinge that is within 1.5 × Inter Quartile Range.

Appendix S4: Trait sources for species

Source code: 1=LEDA (Kleyer et al. 2008); 2=Ecoflora (Fitter & Peat 1994); 3=Bryoatt (Hill et al. 2007); 4=BBS (Atherton et al. 2010); 5= BFNA vol 1 (Ireland 2007); 6=BFNA vol 2 (Ignatov 2009); 7= (Royal Botanic Gardens Kew. 2008); 8= Janecová et al. 2006; 9= Kelber, K.P. & van Konijnenburg-van Cittert, J.H.A. 1998; 10= Juhász et al. 1985; 11= Griffiths & Hemsley 2002.

Abbreviations used: avg = average req = requirements ss = sample size RH = releasing height, est = estimated, img = image, NA = not available.

Nomenclature
Vascular plants: Mossberg & Stenberg (2003)
Bryophytes: Hallingbäck et al. (2006)

Species	SLA (mm^2/mg)	Canopy height (m)	Diaspore mass (mg)
Vascular plants			
Agrostis canina	1	1	1
Agrostis stolonifera	1	1: est from img & RH data	1
Alnus glutinosa	1	1	1
Andromeda polifolia	1	1	1
Betula pubescens	1	1	1
Calamagrostis arundinacea	1	1	1
Calamagrostis arundinacea x *canescens*	1: avg of *C. arundinacea* and *C. canescens*	1: avg of *C. arundinacea* and *C. canescens*	1: avg of *C. arundinacea* and *C. canescens*
Calamagrostis canescens	1	1	1
Calamagrostis epigeios	1	1	1
Calamagrostis purpurea	1	1	1
Calamagrostis stricta	1	1: from *C. varia*	7: from *C. stricta* ssp *inexpansa*
Calluna vulgaris	1	1	1
Cardamine pratensis ssp. *paludosa*	1: from *C. pratensis*	1: from *C. pratensis*	1: from *C. pratensis*
Carex canescens (*curta*)	1	1	1

Carex chordorrhiza	1: Lower req,ss 2	1	1
Carex demissa	1	1	1
Carex dioica	1	1	1
Carex echinata	1: Lower req, ss 3	1	1
Carex elata	1	1	1
Carex flava	1	1: from *C. lepidocarpa*	1
Carex hostiana	1	1	1
Carex lasiocarpa	1	1	1
Carex livida	1: from *C. panicea*	1: from *C. panicea*	1: from *C. panicea*
Carex magellanica	1	1	1
Carex nigra	1	1	1
Carex panicea	1	1	1
Carex pauciflora	1	1	1
Carex pulicaris	1	1	1
Carex rostrata	1	1	1
Carex viridula	1	1	1
Cerastium fontanum	1	1	1
Cirsium arvense	1	1	1
Cirsium helenioides	1	1	1
Cirsium palustre	1	1	1
Comarum palustre	1	1	1
Corallorhiza trifida	NA	NA	7: from *C. striata*
Dactylorhiza incarnata	1	1	8: from *D. majalis* control in Table 4
Deschampsia cespitosa	1	1	1
Deschampsia flexuosa	1	1	1
Drosera intermedia	1: Lower req, ss 4	1	1
Drosera rotundifolia	1	1	1
Dryopteris carthusiana	1	1	1: from *A. diaphanum*
Eleocharis quinqueflora	1	1	1

Empetrum nigrum	1	1	1
Epilobium adenocaulon	1: avg of *E. angustifolium* & *E. palustre*	1: avg of *E. angustifolium* & *E. palustre*	1
Epilobium angustifolium	1	1	1
Epilobium palustre	1	1	1
Epipactis palustris	1	1	7
Equisetum fluviatile	1	1	9
Equisetum palustre	1	1	9
Equisetum pratense	1: avg of *E. fluviatile* & *E. palustre*	1	9
Equisetum variegatum	1: avg of *E. fluviatile* and *E. palustre*	1	9
Eriophorum angustifolium	1	1	1
Eriophorum vaginatum	1: Lower req, ss 3	1	1
Festuca ovina	1	1	1
Filipendula ulmaria	1	1	1
Fragaria vesca	1	1	1
Frangula alnus	1	1	1
Galium boreale	1	1	1
Galium palustre	1	1	1
Galium uliginosum	1	1	1
Geum rivale	1: Lower req, ss 3	1	1
Gymnadenia conopsea	1	1	1
Gymnocarpium dryopteris	1	1	1: from *A. diaphanum*
Hieracium sp.	1: avg of all *Hieracium* spp.	1: avg of all *Hieracium* spp.	1: avg of all *Hieracium* spp.
Huperzia selago	1	1	10
Juncus bufonius	1	2: typical maximum	1
Juncus conglomeratus	1	1	1
Juncus effusus	1	1	1
Juniperus communis	1	1	1
Larix decidua	1	1	1

Linnaea borealis	1	1	1
Luzula multiflora	1	1	1
Luzula pallescens	1: from *L. multiflora*	1: from *L. multiflora*	1
Lycopodium annotinum	1: Lower req, ss 3	1	10
Lycopodium clavatum	1	1	10
Lysimachia thyrsiflora	1	1	1: from *L. vulgaris*
Maianthemum bifolium	1	1	1
Melampyrum pratense	1: Lower req, ss 3	1	1
Melica nutans	1	1	1
Menyanthes trifoliata	1	1	1
Moehringia trinervia	1: Lower req, ss 3	1	1
Molinia caerulea	1	1	1
Myrica gale	1: Lower req, ss 3	1	1
Orthilia secunda	1	1	1
Parnassia palustris	1	1	1
Peucedanum palustre	1	1	1
Phragmites australis	1	1	1
Picea abies	1: Lower req, ss 1-4	1	1
Pinguicula vulgaris	1	1	1
Pinus sylvestris	1	1	1
Poa pratensis	1	1	1
Polygala amarella	1	1	1
Potentilla erecta	1	1	1
Prunus padus	1	1	1
Pyrola rotundifolia	1	1	1: from *P. minor*
Rhododendron tomentosum	1	1	1
Rhynchospora alba	1	1	1
Rhynchospora fusca	1	1	1
Rubus idaeus	1	1	1
Rubus saxatilis	1	1	1

Salix caprea	1	1	1
Salix myrsinifolia	1	1	1: from *S. myrsinites*
Salix repens	1	1	1
Schoenus ferrugineus	1	1	1
Scutellaria galericulata	1	1	1
Selaginella selaginoides	1	1	11
Senecio sylvaticus	1: Lower req, ss 3	1	1
Senecio viscosus	1: Lower req, ss 3	1	1
Solidago virgaurea	1	1	1
Sorbus aucuparia	1: Lower req, ss 3	1	1
Stellaria longifolia	1: avg of all *Stellaria* spp.	1	1
Taraxacum vulgare	1:avg of all *Taraxacum* spp.	1:avg of all *Taraxacum* spp.	1
Trichophorum alpinum	1: from *C. dioica*	1: from *C. dioica*	1: from *T. cespitosum*
Trichophorum cespitosum	1: from *C. dioica*	1: from *C. dioica*	1
Trientalis europaea	1	1	1
Tussilago farfara	1	1	1
Typha latifolia	1	1	1
Utricularia intermedia	1: avg of all *Utricularia* spp.	1	NA
Vaccinium myrtillus	1	1	1
Vaccinium oxycoccos	1	1	1
Vaccinium uliginosum	1	1	1
Vaccinium vitis-idaea	1	1	1
Valeriana sambucifolia	1	1	1
Viburnum opulus	1	1	1
Vicia cracca	1	1	1
Viola canina ssp. *montana*	1: from *V. canina*	1	1
Viola epipsila	1: avg of all *Viola* spp.	1	NA
Viola palustris	1	1	1
Viola riviniana	1	1	1

Bryophytes		
Aneura pinguis	3	3
Aulacomnium androgynum	3	3
Aulacomnium palustre	3	3
Brachytheciastrum velutinum	3	3
Brachythecium albicans	3	3
Brachythecium oedepodium	3: avg of *Brachythecium*	3: avg of *Brachythecium*
Brachythecium reflexum	3	3
Brachythecium rutabulum	3	3
Brachythecium salebrosum	3	3
Bryum pseudotriquetrum	3	3
Calliergon cordifolium	3	3
Calliergonella cuspidata	3	3
Campyliadelphus elodes	3	3
Campylium protensum	3	3
Campylium stellatum	3	3
Cephalozia cf. *bicuspidata*	3	3
Cephalozia connivens	3	3
Cephalozia pleniceps	3	3
Cephalozia sp.	3: avg of *Cephalozia*	3: avg of *Cephalozia*
Cephaloziella sp.	3: avg of *Cephaloziella*	3: avg of *Cephaloziella*
Ceratodon purpureus	3	3
Chiloscyphus pallescens	3	3
Chiloscyphus polyanthos	3	3
Cinclidium stygium	3	3
Climacium dendroides	3	3
Dicranella heteromalla	3	3
Dicranella sp.	3: avg of *Dicranella*	3: avg of *Dicranella*
Dicranum bonjeanii	3	3

Dicranum fuscescens/flexicaule	3	3
Dicranum majus	3	3
Dicranum montanum	3	3
Dicranum polysetum	3	3
Dicranum scoparium	3	3
Dicranum undulatum	5	3
Drepanocladus polygamus	3	3
Fissidens adianthoides	3	3
Fissidens osmundoides	3	3
Helodium blandowii	3	3
Herzogiella seligeri	3	3
Hylocomium splendens	3	3
Hypnum cupressiforme	3	3
Kindbergia praelonga	6	NA
Lepidozia reptans	3	3
Lophocolea heterophylla	3	3
Mnium hornum	3	3
Oncophorus virens	3	3
Pellia cf. *epiphylla*	3	3
Plagiomnium elatum	3	3
Plagiomnium elipticum	3	3
Plagiothecium curvifolium	3	3
Plagiothecium denticulatum var. *undulatum*	3: from *P. denticulatum*	3: from *P. denticulatum*
Pleurozium schreberi	3	3
Pohlia cf. *nutans*	3	3
Polytrichastrum formosum	3	3
Polytrichastrum longisetum	3	3
Polytrichum commune	3	3
Polytrichum juniperinum	3	3

Polytrichum strictum	3	3
Preissia quadrata	3	3
Ptilidium pulcherrimum	3	3
Rhizomnium pseudopunctatum	3	3
Rhizomnium punctatum	3	3
Rhodobryum roseum	3	3
Rhytiadelphus squarrosus	4	3
Riccardia cf. *chamaedryfolia*	3	3
Riccardia cf. *latifrons*	3	3
Riccardia multifida	3	3
Sanionia uncinata	3	3
Scapania irrigua	3	3
Scapania paludicola	3	3: avg of *Scapania*
Scorpidium cossonii	3	3: avg of *Scorpidium*
Scorpidium scorpioides	3	3
Sphagnum angustifolium	3	3
Sphagnum capillifolium	3	3
Sphagnum centrale	3	3
Sphagnum compactum	3	3
Sphagnum contortum	3	3
Sphagnum fallax	3	3
Sphagnum fimbriatum	3	3
Sphagnum flexuosum	3	3
Sphagnum fuscum	3	3
Sphagnum girgensohnii	3	3
Sphagnum magellanicum	3	3
Sphagnum palustre	3	3
Sphagnum papillosum	3	3
Sphagnum platyphyllum	3	3
Sphagnum riparium	3	3

Sphagnum rubellum	3	3
Sphagnum russowii	3	3
Sphagnum squarrosum	3	3
Sphagnum subfulvum	3: avg of *Sphagnum*	3: avg of *Sphagnum*
Sphagnum subnitens	3	3
Sphagnum subsecundum	3	3
Sphagnum teres	3	3
Sphagnum warnstorfii	3	3
Sphagnum wulfianum	3: avg of *Sphagnum*	3: avg of *Sphagnum*
Splachnum ampullaceum	3	3
Straminergon stramineum	3	NA
Warnstorfia exannulata	3	3

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Appendix S5: Table showing result from the Wilcoxon 2-sample test comparing the restoration treatments with the reference site.

Wilcoxon 2-sample test, showing differences in functional diversity indices and community weighted mean (CWM) of functional traits and species richness between each restoration treatment and the reference site for the joint analyses (All) and the vascular plant analyses (VP) at year 8. FRic= Functional richness, FDiv=Functional divergence, FDis=Functional dispersion, CH= Canopy height, DM=Diaspore mass, SLA=Specific leaf area and W= Wilcoxon test statistic.

		All		VP	
		Cut	**Rewetted**	**Cut**	**Rewetted**
FRic	W	13	25	23	22
	p	0.01	0.06	0.04	0.03
FDiv	W	26	35	55	64
	p	0.07	0.22	0.97	0.53
FDis	W	0	0	0	0
	p	1.49E-05	1.49E-05	3.61E-04	3.61E-04
CH	W	0	2	0	0
	p	1.49E-05	5.94E-05	3.61E-04	3.61E-04
DM	W	60	64	63	63
	p	0.72	0.54	0.57	0.57
SLA	W	NA	NA	74	58
	p	NA	NA	0.19	0.82
Species richness	W	88.00	88.00	82.00	79.00
	p	0.02	0.02	0.06	0.09

Appendix S6: Trait sources for species, Criteria used in LEDA and hierarchies of sources.

Trait sources for species

Source code: 1=LEDA (Kleyer et al. 2008); 2=Ecoflora (Fitter & Peat 1994); 3=Bryoatt (Hill et al. 2007); 4=BBS (Atherton et al. 2010); 5= BFNA vol 1 (Ireland 2007); 6=BFNA vol 2 (Ignatov 2009); 7= (Royal Botanic Gardens Kew. 2008); 8= Janecová et al. 2006; 9= Kelber, K.P. & van Konijnenburg-van Cittert, J.H.A. 1998; 10= Juhász et al. 1985; 11= Griffiths & Hemsley 2002.

Abbreviations used: avg = average req = requirements ss = sample size RH = releasing height, est = estimated, img = image, NA = not available.

Criteria used in Leda

SLA
Leaf rehydration prioritized. If not available "No leaf rehydration" or "Unknown". Values from "Leaf hydration" and "No leaf hydration" were never mixed. Weighted averages with sample size as weight used when several values were present.

Canopy height:
Max value used. Highest value used when several records existed.

Diaspore mass:
Minimum sample size 5 prioritized. Mean value, Air dried, Germinule, Actual measurements, Largest number of replicates, If several values existed the highest mean value was used

Hierarchies of sources

Numbers refer to Source code in 1:1.

Vascular plants

Diaspore mass: LEDA (1) →Kew Seed Database (7) →species specific sources (8), (9), (10), (11)
Canopy height: LEDA (1) → Ecoflora (2)
SLA: LEDA (1)

Bryophytes

Canopy height: Bryoatt (3) → BBS (4) → BFNA (5 and 6)
Diaspore mass: Bryoatt (3)

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CHAPTER IV

Functional diversity analysis helps to identify filters affecting community assembly after fen restoration by top-soil removal and hay transfer

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ABSTRACT

Top-soil removal followed by species introduction through hay transfer has appeared as a method to restore drained fens. This method addresses abiotic constraints by restoring hydrology and nutrient status, and biotic constraints by removing an unwanted seed bank and counteracting dispersal-limitation. Restoration works by altering environmental filters. Knowledge about the restoration actions effect on functional traits is necessary to understand which types of species may establish. In this study we analyse which factors in top-soil removal followed by hay transfer influence selection and composition of functional traits. Top-soil removal followed by hay transfer from reference sites was conducted at two sites in the Całowanie fen, 33 km SE of Warsaw, Poland. Species and abundance data were recorded for three consecutive years. These data, combined with data on functional traits were used to analyse the effect of the restoration actions on four functional diversity-indices and the community weighted mean of functional traits. Our results reveal a strong habitat filter in the restoration site that follows an elevation gradient. At low elevation this filter selects low values of autochory and specific leaf area and high values of clonal lateral spread, Ellenberg moisture values, and dispersal through hydrochory. The transferred hay differs in trait characteristics compared to the reference site vegetation by having species of higher specific leaf area, lower Ellenberg moisture value and lower dispersal by autochory and hydrochory. The result presented here has three important implications for fen restoration. First, the difference in trait-characteristics between the transferred hay and the reference site it was harvested from limits the restoration potential. Second, since for several fen species important functional traits are filtered along an elevation-gradient, careful planning regarding depth of top-soil removal is needed. Finally the results illustrate how a functional analysis can be used to detect environmental filters acting during ecological restoration.

Introduction

Ecological restoration has a high failure rate (Benayas et al. 2009). The failure to restore a community is many times caused by one or more environmental filters that constrain the restored community from approaching the state of the reference community (Myers and Harms 2009). These filters can be abiotic habitat filters, (e.g. flooding and anoxia), biotic filters (e.g. competition) or dispersal filters (Keddy 1992). In order to improve restoration outcomes, it is important to understand what constrains the restored ecosystem from reaching the state of the reference system. While traditional evaluations of success, based on species identity and abundance did not provide us with an ecological explanation to why certain species successfully establish at the restoration site, while others do not, the advent of functional diversity to community ecology has provided a promising tool for such an analysis (Funk et al. 2008; Hedberg and Kotowski 2010; Hedberg et al. 2013). A classical species identity-focused analysis provides information on how restoration measures or environmental factors affect certain species or communities. However, it does not provide an ecological explanation for these changes, and the results risk being limited by the geographic boundary of the species studied. Switching focus from species to traits that are relevant for the studied ecosystem adds an ecological explanation to observed changes in species composition caused by restoration actions. Ecological restoration is at its very base a method to assist community recovery by changing environmental filters (abiotic, biotic or dispersal) that control the species composition (Myers and Harms 2009). By analysing occurrence of specific traits in a community we can detect environmental filters that operate on them (Diaz et al. 2007),

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whereas functional diversity indices (e.g. Mason et al. 2005) can help to assess the relative importance of habitat versus competition filtering (e.g. Kotowski et al. 2010). Yet, despite the advance of functional ecology, its tools are little used in ecological restoration. In this study we employ them to analyse filtering mechanisms operating during early stages of rich fen restoration by top-soil removal and hay-transfer. Specifically, we want to test whether habitat or competition filtering prevails during restoration.

In riparian fen vegetation, both habitat factors (soil anoxia) and competition for light have been identified as strong environmental filters (Kotowski and van Diggelen 2004; Kotowski et al. 2010), while the dispersal capacity of target species has been found to additionally constrain the restoration process (Klimkowska et al. 2007). An increasingly applied method to restore the hydrology and low trophic status of drained fens, and at the same time counteract dispersal limitation of target species, is to remove the degraded mineralised peat and introduce target species from reference-sites via hay-transfer (Klimkowska et al. 2010a; Rasran et al. 2007). From a filter perspective, top-soil removal should reduce competition compared to degraded sites by removing excess N and P and eliminating potential competitors from the seed bank and standing vegetation. Top-soil removal simultaneously exposes water-saturated peat soils, which increases the abiotic filter of anoxia (habitat filtering sensu Cornwell et al. 2006). Anoxia can further decrease competition filtering by lowering the growth rate of all species during seedling recruitment (Kotowski et al. 2010). Therefore, we hypothesise that competition filtering is lowest in sites, where degraded peat is removed down to the saturated layer, where habitat filtering dominates. This balance is supposed to change in favour of competition filtering if top-soil removal was shallower and an aerated layer remained. In heavily degraded fen sites, such as our area prior to restoration as well as areas at our site that were not restored, we expect that functional diversity is generally low due to habitat filtering by other stress factors, such as draught and K limitation (Van Duren et al. 1997). The second measure, the transfer of hay, is specifically applied to combat the dispersal limitation of the target species. We therefore hypothesise that it will increase functional diversity (as more species can potentially establish). Alternatively, however, it could decrease diversity by increasing competition filtering, when competitive species are introduced with hay.

We aim to test the above predictions with the analysis of community weighted means (CWM) (Garnier et al. 2004, 2007) of the functional traits, which are supposed to determine species response to the analysed environmental filters, and their functional diversity indices proposed by Mason et al. (2005) and Laliberté and Legendre (2010).

The four functional diversity indices we use measure different aspects of functional diversity. Functional richness (FRic) measures the size of the filled niche space. For a single trait it is the difference between the maximum and minimum value of the trait, whereas for two or more traits it is the minimum area (two traits) or volume (more than two traits) that covers all trait values (Mason et al. 2005; Villéger et al. 2008). Functional evenness (FEve) is a measure of how evenly the biomass of a community is distributed within a niche-space. Assuming evenly distributed resources, a low FEve indicates, that some parts of the niche space are under-utilised, which increases risk of invasion of new species (Mason et al. 2005). Functional divergence (FDiv) measures the distribution of abundance within a niche-space. For a single trait, high FDiv occurs when the most abundant species have trait-values on the extreme ends of the trait-axis (Mason et al. 2005; Villéger et al. 2008). In a multivariate context, FDiv is measured as the average distance of each species to the centre of gravity of the trait-space (Villéger et al. 2008). Functional dispersion (FDis) is similar to FDiv in that it measures dispersion in a multivariate trait-space as the average distance of each species to a centre-point. The two indices differ in that FDiv measures the average distance of each species to the centre of gravity of the trait space, whereas FDis measures the average distance of each species to the centroid of all species. FDis is independent of the convex hull concept, which makes it less sensitive to outliers compared to the other three functional diversity indices (Laliberté and Legendre 2010). Community weighted mean (CWM) is a measure of the dominant trait-value in a community (e.g. Garnier et al. 2004, 2007; Diaz et al. 2007).

Based on the structure and functioning of the functional diversity indices, we assume that low habitat filtering can be detected by high values of FRic and FDis when tested against a restoration action or an abiotic variable associated with the restoration action. Increased competition should be expressed in increased FEve and FDiv. The functional analysis is used as a complement to the classical analysis that presents the results in averages of species richness, as well as ordination techniques for the restored, reference and control communities.

Methods

Study site

Całowanie fen (52° 0′41.80″N, 21°21′11.26″E), 33 km SE of Warsaw, Poland is a soligenous former rich fen in the Wisła ice-marginal valley (Oświt and Dembek 2001; Żurek 1990). The average temperature for Jun–Aug is 17.5 °C, and the average temperature for Dec–Feb is −2.5 °C, while the average annual rainfall is 555 mm (Olszewski 2003). Due to degradation caused by drainage, the site has a large seasonal groundwater level variation (Klimkowska et al. 2010a). Prior to the restoration, the degraded parts where top-soil removal was carried out, had vegetation dominated by *Urtica dioica* L., *Festuca rubra* L., *Anthoxanthum odoratum* L. and *Salix cinerea* L.

Experimental design

Two areas of 0.5 ha each were restored through top-soil removal followed by hay-transfer. These sites are hereafter referred to as the restoration-sites. The top-soil was removed in December 2008 with an average depth of 60 cm. The surface of the restoration sites was not levelled, and both restoration sites had a significant within site variation in elevation. This elevation gradient, connected with a gradient in moisture (or flooding depth), was used as a predicting abiotic factor in our analyses.

In spring and early summer of 2009 two nearby donor meadows (hereafter referred to as reference sites) were monitored for species presence and abundance. One reference site was mown in August 2009 and the other was mown in September 2009. Samples of the mown hay from both reference sites were collected for a species content analysis. The species content analysis was done by incubating eight trays with hay spread over commercial peat-soil (with a control for species content in the soil) in a greenhouse and a climate-chamber and identifying emerging seedlings, whose abundance was estimated using the Londo scales (Londo 1976). After mowing, the restoration sites were divided into 15 m wide belts, and hay was spread evenly on every second belt. Within each belt two 2 m × 2 m permanent plots were placed out.

Control plots (five with – and five without hay transfer) were placed on degraded sites (hereafter referred to as the control sites) adjacent to each of the two restoration site. Five plots were placed at each of the two reference sites as well. Monitoring of the full control plots (control-plots without hay-transfer) and the reference sites started one year later than other plots. Due to boars (*Sus scrofa* L.) destroying 10 plots in one control site (five plots with hay transfer

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and five plots without hay transfer) between the second and third year, these plots were removed from the analysis for all years.

Plots were monitored Jun–Aug in 2009, 2010 and 2011 (hereafter referred to as year 1, year 2, and year 3) for abundance of vascular plant species using the Londo-scale (Londo 1976). Species names for vascular plants follow Jäger and Werner (2009). Since sedges were a target group of the restoration, and early results showed clear failure of their establishment, an additional directed introduction of locally collected seeds of *Carex diandra* Schrank., *C. rostrata* Stokes and *C. nigra* L., Reichard. was conducted in the winter of year 2 in the restoration sites. Each 2 m × 2 m permanent plot had its elevation relative to the groundwater level measured in the third year through laser nivelation (Topcon RL-100 1S).

Since our permanent plots did not cover the whole elevation gradient present within the restoration sites, we carried out an additional grid-based analysis in the summer of year 3 of the distribution of 14 selected species characteristic for fens, fen meadows and degraded fens. This was done by dividing both restoration sites in a 15 m × 4 m grid. Species abundance was recorded in a categorical scale with the categories "absent", "present" (cover up to 10%) and "abundant" (cover above 10%). Each plot's elevation was calculated as an average from four point measurements.

Data analysis

Prior to statistical analysis, the abundance data given in Londo decimal scale was transformed into percentages. Community development of the different treatments was examined in a RDA using Canoco 4.51 for Windows (Ter Braak and Šmilauer 2003). To analyse the effect of environmental filters on community assembly, the functional diversity indices functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) (Villéger et al. 2008) and functional dispersion (FDis) (Laliberté and Legendre 2010) as well as community weighted mean (CWM) (Diaz et al. 2007; Garnier et al. 2004, 2007) of the analysed traits were calculated using the package FD (Laliberté and Legendre 2010; Laliberté and Shipley 2010) in the statistic program R (R Development Core Team 2012).

The analysed traits were specific leaf area (SLA), canopy height, Ellenberg moisture values (EMV), clonal lateral spread (CLS) and dispersal mode. SLA separates plants in terms of photosynthesis-investments (Wright et al. 2004a), relative growth rate, (Wright and Westoby 2001) shade tolerance, (Janse-ten Klooster et al. 2007), flood tolerance, (Violle et al. 2011) leaf-anoxia tolerance (Mommer et al. 2006) and resource use (Wilson et al. 1999; Wright et al. 2004b). Species with a high specific leaf area (SLA) have a higher metabolic activity and are often species that are ruderals or competitors, and rarely stress tolerators (Pierce et al. 2007). Canopy height is an important trait in the competition for light e.g. (Hautier et al. 2009). EMV is included here as an indication of adaptation to wet conditions. Ellenberg assigned the indicator values to natural developed communities (Ellenberg et al. 1992), and its high values indicate plant's tolerance to anoxia. The capacity for CLS is common among wetland vascular plants, and is necessary to dominate the vegetation (Grime 1987). It separates ruderal plants, interstitial plants and matrix plants (Boutin and Keddy 1993), and explains most of the variation between different types of clonal growth organs among wetland plants (Sosnová et al. 2010). Dispersal mode can help to identify filters limiting species arrival to the restoration site e.g. (Ash et al. 1994; Bradshaw 1983; Wagner 2004).

SLA and canopy height data follow LEDA Trait base (Kleyer et al. 2008). For a few species missing in LEDA, data on taxonomically and anatomically similar species were used as an approximation. Three values were based on expert judgment. EMV were taken from PLANTATT (Hill et al. 2004), except for five values taken from Floraweb (Bundesamt für Naturschutz 2011). Data on CLS are derived from CLO-PLA (Klimešová and De Bello 2009; Klimešová and Klimeš), after transforming it into a binary trait, where species with a max CLS-capacity of <0.01 or 0.01–0.25 were given the value 0, and species with a max CLS-capacity of >0.25 or dispersible were given the value 1. For the few species missing in CLO-PLA, expert judgment was used. The dispersal mode data follow Floraweb (Bundesamt für Naturschutz 2011), except for three values taken from LEDA (Kleyer et al. 2008). This trait was coded as a dummy-variable with four categories (anemochory, hydrochory, autochory and animal dispersal (including anthropochory)). Traits were weighted for the calculation of FD-indices, so that the sum of the weights of the dummy-trait categories equalled the weight of one whole trait. The CWM of dummy-traits was expressed in percentage. FDis, FEve, FDiv and CWM of the traits were weighted by the relative species abundance. FRic was standardised by the 'global FRic' that contains all species, so that FRic was constrained between 0 and 1.

The influence of hay-transfer and elevation in the restoration sites were tested with a linear mixed effect model using the lme function in the nlme package (Pinheiro et al. 2012) in R (R Development Core Team 2012). Response variables were FRic, FEve, FDiv, FDis and CWM of the traits SLA, canopy height, EMV, CLS and dispersal mode. Fixed factors were year, hay-transfer, elevation (plots elevation above groundwater level) and the interactions year × hay-transfer, year × elevation, hay-transfer × elevation and year × hay-transfer × elevation. To account for temporal autocorrelation the id-number of each plot was used as a random factor nested under year. To achieve normal distribution of residuals, data for canopy height had to be log transformed, and data for autochory and hydrochory had to be square-root transformed. To account for multiple testing, a Bonferroni correction was applied with the significance-level $0.05/n_y$, with $n_y = 12$ (4 fd indices, 4 full traits and 4 dummy-traits).

To assess the effectiveness of hay-transfer, the functional traits at the reference sites at year 3 were tested against the data from the hay-sample species content analysis. Since different abundance scales were used for field monitoring (Londo coverage), and the species content analysis of the hay-samples (Londo abundance; r, p, a, m), they were merged into an abundance scale of 1 to 4, where 0.1 in releves and r in trays = 1, 0.2–0.4 in releves and p in trays = 2, 1 in releves and a in trays = 3 and >1 in releves and m in trays = 4. To account for bias in our merged scale the results were compared to a test where only presence/abundance data were used in a two sampled Wilcoxon test. To account for multiple testing, a Bonferroni correction was applied with the significance-level $0.05/n_y$, with $n_y = 12$ (4 FD indices, 4 full traits and 4 dummy-traits).

The species specific response of the 14 selected species to the elevation gradient was analysed using a Generalised Additive Model in CANOCO (Ter Braak and Šmilauer 2003), with an assumed Poisson distribution and a Bonferroni correction applied with a significance-level of $0.05/n_y$ with $n_y = 14$.

All trait-values for all species, information on species present for each treatment, criterions used in LEDA and full result tables for all years are available as an online supplementary file.

Results

Changes in species number

The only significant change in species number between the first and third year occurred for top-soil removal without hay dispersal where species richness increased from 10.15 ± 1.19 SE to 13.50 ± 1.09 SE (2 sampled Wilcoxon test, p = 0.02, W = 100.5). A comparison between the treatments for the third year shows that

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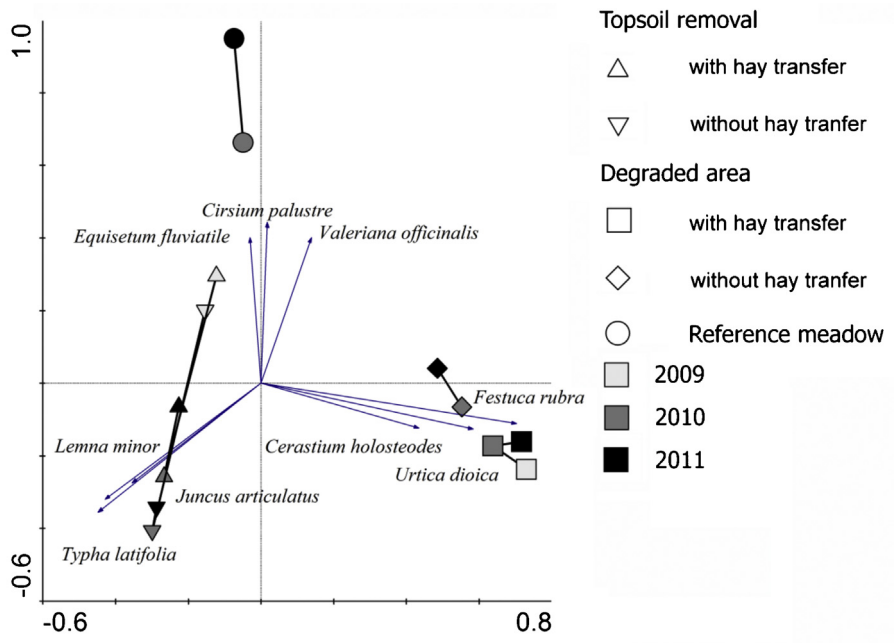

Fig. 1. Redundancy analysis of the plant composition for plots with top-soil removal with and without hay-transfer, degraded meadows with and without hay-transfer and reference meadow for year 1 (2009), year 2 (2010) and year 3 (2011).

the only significant difference in species richness between treatments exists between the reference sites that had a species richness of 16.00 ± 1.32 SE and the full control plots that had a species richness of 10.20 ± 2.01 SE (2 sampled Wilcoxon test, p = 0.02, W = 44.5). The highest average species number at year 3 was recorded at the reference-sites.

Vegetation changes

The first two axes of the redundancy analysis explain 24.7% and 4.3% of the species variance respectively. The reference site and restoration treatments are near each other and clearly separated from the control plots along the first axis, which clearly expresses the moisture gradient (Fig. 1).

Functional analysis of the major treatments

A comparison between the different treatments functional diversity and community weighted means (CWM) of functional traits at year 3 show that Ellenberg moisture value (EMV), hydrochory and functional dispersion (FDis) were significantly higher in the restoration sites and reference sites than in the control sites (Table 1). Clonal lateral spread (CLS), functional evenness (FEve) and functional divergence (FDiv) were significantly higher in the restoration sites compared to the control sites (Table 1). Anemochory and animal dispersal were significantly higher in the control sites compared to the restoration sites and reference sites (Table 1). Autochory was significantly higher in the reference sites compared to the restoration sites and control sites (Table 1).

Table 1
The response of functional traits to major treatments at Year 3 (2011). P = *p*-value from Wilcoxon 2-sample test (Wx). W = W-values from Wilcoxon signed-rank test. Bonferroni correction α/n_y applied ($\alpha = 0.05$, $n_y = 12$). Statistically significant effects are followed by *. EMV = Ellenberg moisture value, CLS = Clonal lateral spread, Ane = Anemochory, Ani = Animal dispersal, HC = Hydrochory, AC = Autochory, FEve = Functional evenness, FDiv = Functional divergence, FDis = Functional dispersion. REST = Restoration-site, REF = Reference-site, CTRL = Control-site, SE = Standard error.

FD-index	Test	Year 3		REST		REF		CTRL	
		p	*W*	Mean	SE	Mean	SE	Mean	SE
CWM EMV	REST × CTRL REF × CTRL	1.16E−08* 1.08E−05*	364 0	8.91	0.18	8.65	0.19	6.04	0.22
CWM CLS	REST × CTRL	1.04E−07*	358	0.7	0.04	0.43	0.09	0.11	0.04
CWM Ane	REST × CTRL REF × CTRL	2.38E−06* 1.82E−04*	3 100	0.68	0.03	0.72	0.05	0.97	0.01
CWM Ani	REST × CTRL REF × CTRL	5.38E−06* 1.05E−03*	28 91	0.61	0.03	0.6	0.08	0.87	0.04
CWM HC	REST × CTRL REF × CTRL	4.24E−05* 3.25E−04*	343 6	0.25	0.03	0.32	0.09	0.03	0.01
CWM AC	REST × REF REF × CTRL	2.59E−08* 1.08E−05*	8 0	0.16	0.02	0.61	0.06	0.09	0.02
FEve	REST × CTRL	1.18E−03*	30	0.62	0.01	0.66	0.05	0.49	0.04
FDiv	REST × CTRL	1.46E−03*	303	0.89	0.01	0.82	0.03	0.77	0.03
FDis	REST × CTRL REF × CTRL	1.65E−05* 3.25E−04*	336 6	0.15	0.01	0.16	0.01	0.08	0.01

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Table 2
Differences in functional diversity indices and community weighted mean (CWM) of functional traits between hay samples from the transferred hay, and the reference site in year 3 (2011). Wilcoxon 2-sample test used. Bonferroni correction applied with the significance level set to α/n_y ($\alpha = 0.05$, $n_y = 12$). Statistically significant effects are followed by *. REF = Reference-sites, FRic = Functional richness, SLA = Specific leaf area, EMV = Ellenberg moisture value, HC = Hydrochory, AC = Autochory, SE = Standard error and w = W-values from Wilcoxon signed-rank test. Mean and SE are given in merged Londo cover and Londo abundance scale values were 0.1 and r = 1, 0.2–0.4 and p = 2, 1 and a = 3 and > 1 and m = 4.

Index	REF				Hay sample	
	P	*w*	Mean	SE	Mean	SE
FRic	4.28E−04*	143	5.38E−04	1.15E−04	1.15E−04	1.90E−05
CWM SLA	4.52E−06*	4	22.64	0.89	28.59	0.61
CWM EMV	2.77E−05*	160	8.28	0.18	6.64	0.14
CWM HC	1.30E−04*	153	0.27	0.05	0.09	0.01
CWM AC	1.07E−04*	154	0.45	0.03	0.23	0.02

Table 3
Species specific response to differences in elevation above the groundwater level. Bonferroni correction applied, with the significance level set to α/n_y ($\alpha = 0.05$, $n_y = 14$). Statistically significant effects are followed by *.

Species	Response type	*F*	*p*
Typha latifolia	Limnic	14.91	<1.0e−6*
Carex pseudocyperus	Fen	11.09	<1.0e−6*
Carex rostrata	Fen	4.09	7.7e−3
Juncus articulatus	Fen	32.46	<1.0e−6*
Lythrum salicaria	Fen	12.26	<1.0e−6*
Salix cinerea	Fen	18.32	<1.0e−6*
Deschampsia caespitosa	Wet meadow	28.65	<1.0e−6*
Eleocharis palustris	Wet meadow	4.46	3.6e−2
Holcus lanatus	Wet meadow	19.74	1.3e−5*
Lotus pedunculatus	Wet meadow	42.05	<1.0e−6*
Potentilla anserina	Wet meadow	23.07	<1.0e−6*
Ranunculus lingua	Wet meadow	12.34	5.41e−4*
Ranunculus repens	Wet meadow	69.49	<1.0e−6*
Sagina nodosa	Wet meadow	49.08	<1.0e−6*

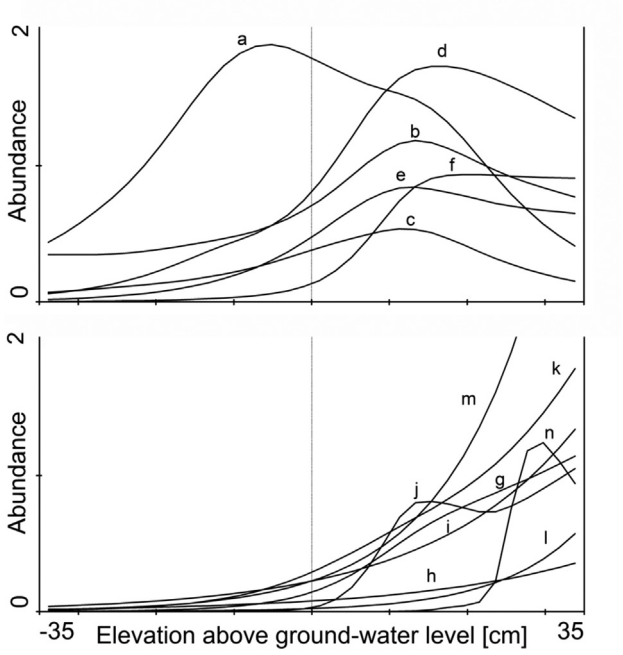

Fig. 2. Species specific response of abundance to elevation above the groundwater level for **a**: *Typha latifolia*, **b**: *Carex pseudocyperus*, **c**: *Carex rostrata*, **d**: *Juncus articulatus*, **e**: *Lythrum salicaria*, **f**: *Salix cinerea*, **g**: *Deschampsia caespitosa*, **h**: *Eleocharis palustris*, **i**: *Holcus lanatus*, **j**: *Lotus pedunculatus*, **k**: Potentilla anserina, **l**: *Ranunculus lingua*, **m**: *Ranunculus repens*, **n**: *Sagina nodosa*. Upper graph: limnic and fen species, Lower graph: wet meadow species.

Effects of hay transfer

Samples from the transferred hay grown in trays had a significantly higher specific leaf area (SLA), and a significantly lower EMV, autochory and hydrochory, as well as a lower functional richness (FRic) than the vegetation the hay was harvested from (Table 2). This result was not changed if the merged scale was replaced by presence/abundance data.

Species specific response to the elevation gradient

All except two species reacted significantly to differences in plot elevation (Table 3). The responses can be divided into three groups: "limnic species"; "fen species" (many of which were the target of the restoration); and, "wet meadow species" (Fig. 2).

Functional analysis of the restored sites

Elevation significantly affected autochory, CLS, EMV, hydrochory, SLA, FDis and FRic. Autochory, SLA, FDis and FRic increased with increasing elevation, whereas CLS, EMV and hydrochory decreased with increasing elevation (Table 4, Fig. 3a–g). Hay

Table 4
The effect of abiotic/biotic parameters on functional diversity indices and community weighted mean (CWM) of functional traits. Bonferroni correction applied with the significance level set to α/n_y ($\alpha = 0.05$, $n_y = 12$). Tr = Transformation, sqrt = square root, minus sign = no transformation, AC = Autochory, CLS = Clonal lateral spread, EMV = Ellenberg moisture values, HC = Hydrochory, SLA = Specific leaf area, FDis = Functional dispersion, FRic = Functional richness, FEve = Functional evenness, FDiv = Functional divergence, num DF = numerator degrees of freedom, den DF = denominator degrees of freedom.

Index	Tr	Interaction	num DF	den DF	*F*	*P*
CWM AC	sqrt	Elevation	1	33	17.93	0.0002*
CWM CLS	–	Elevation	1	33	112.92	<0.0001*
CWM EMV	–	Elevation	1	33	49.16	<0.0001*
CWM HC	sqrt	Elevation	1	33	41.43	<0.0001*
CWM SLA	–	Elevation	1	33	14.49	0.0006*
FDis	–	Elevation	1	33	12.87	0.0011*
FRic	–	Elevation	1	33	14.87	0.0005*
CWM CLS	–	Hay treatment	1	33	18.05	0.0002*
FEve	–	Hay treatment	1	30	10	0.0036*
FEve	–	Hay treatment × Elevation	1	30	12.27	0.0015*
FDiv	–	Year × Hay treatment	2	58	11.34	0.0001*

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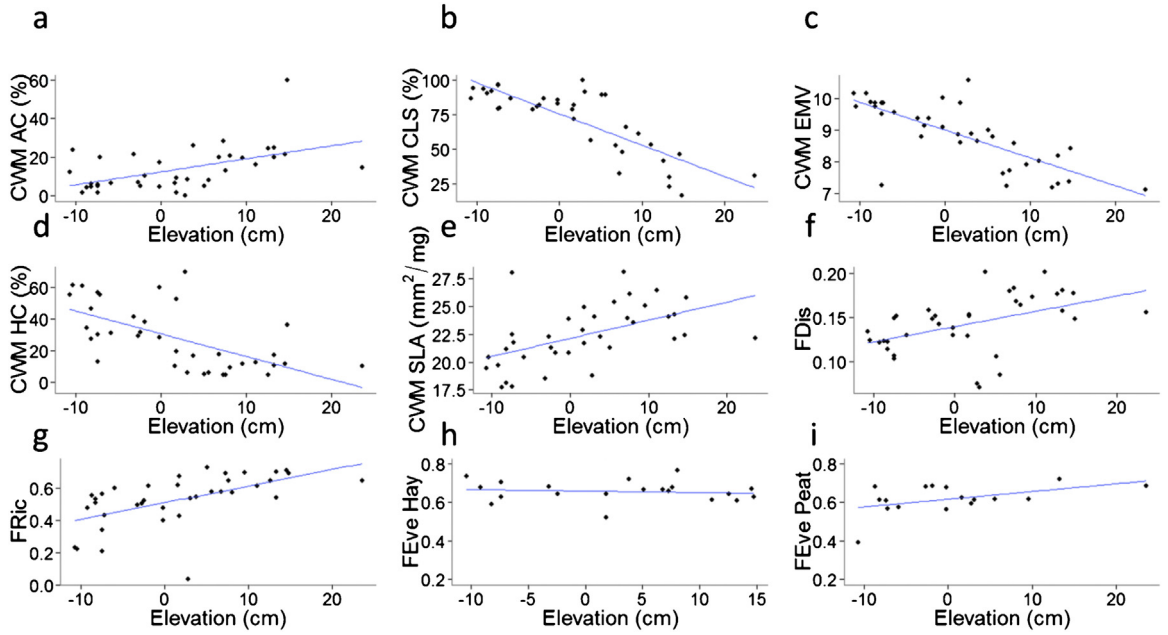

Fig. 3. **a**–**i**: The interaction within the restoration sites between elevation above the groundwater level and **a**) Autochory (AC) **b**) Clonal lateral spread (CLS) **c**) Ellenberg moisture value (EMV) **d**) Hydrochory (HC) **e**) Specific leaf area (SLA) **f**) Functional dispersion (FDis) **g**) Functional richness (FRic), as well as the interaction between hay transfer and elevation on functional evenness (FEve), were **h**) with hay transfer, and **i**) without hay transfer.

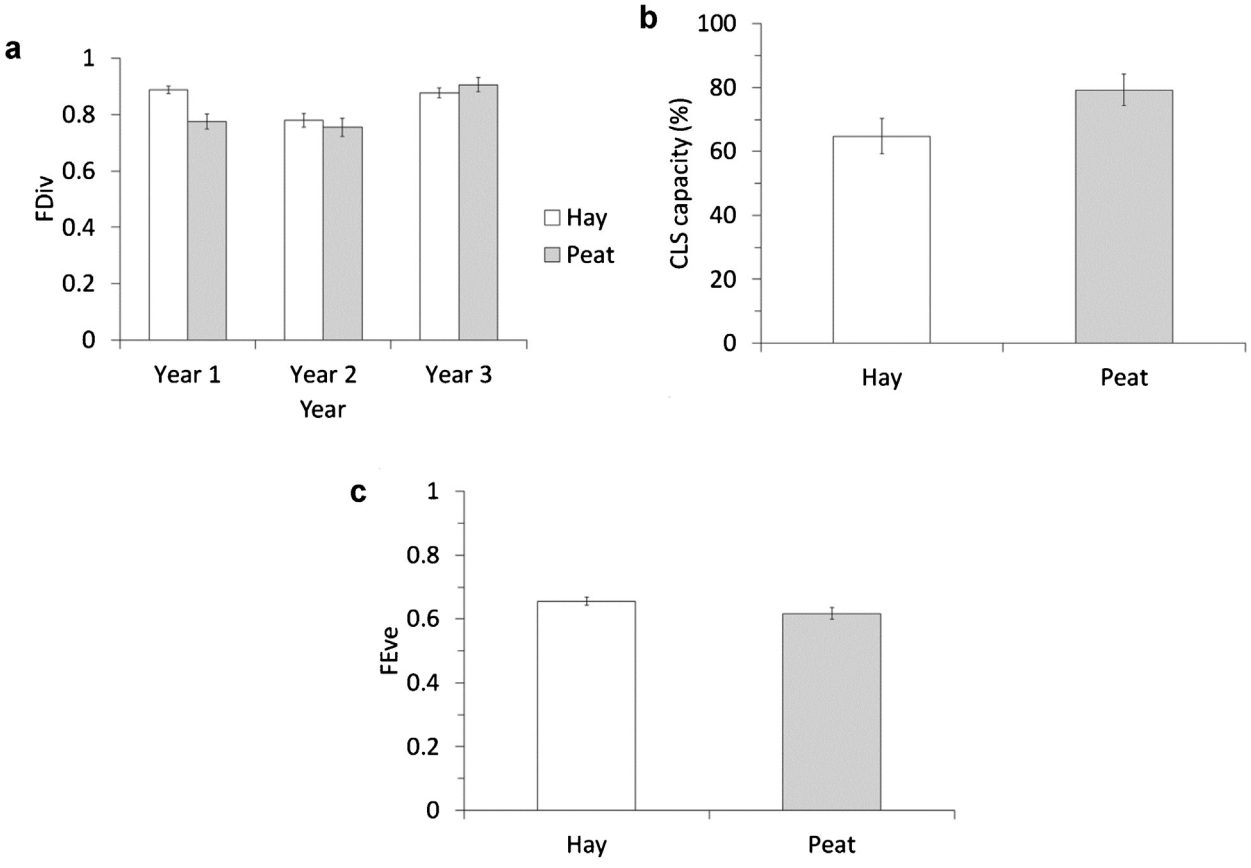

Fig. 4. Effect of hay transfer **a**) The interaction between hay transfer and time on functional divergence (FDiv). **b**) The effect of hay transfer on clonal lateral spread (CLS). **c**) The effect of hay transfer on functional evenness (FEve).

dispersal caused a significant decrease in CLS-capacity (Table 4, Fig. 4b) and a significant increase in FEve (Table 4, Fig. 4c). There was also a significant interaction between hay dispersal and elevation on FEve, with FEve increasing with increasing elevation on plots without hay transfer, whereas hay transfer reduced this effect of elevation (Table 4, Fig. 3h–i). FDiv had a significant interaction with hay dispersal and time, with increased FDiv during the first year on plots that received hay (Table 4, Fig. 4a). The difference in

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FDiv between the hay plots and no hay plots decreased with time, and in the third year the plots that received hay had a marginally lower FDiv than the plots that did not receive hay.

Discussion

Effectiveness of hay transfer

The significantly higher specific leaf area (SLA) and significantly lower Ellenberg moisture value (EMV) found in the transferred hay indicates that the hay contained on average seeds of more ruderal and/or competitive species (Pierce et al. 2007) adapted to drier conditions (Ellenberg et al. 1992) than what is found at the reference site from where the hay was harvested. Among species that are disfavoured by this are *Carex* species, which in our study have lower SLA (average for *Carex*: 18.03 mm^2/mg, average for all species: 24.03 mm^2/mg) and higher EMV (average for *Carex*: 8.57, average for all species: 7.10) and a higher degree of autochory (average for *Carex*: 85.71%, average for all species: 18.60%) and hydrochory (average for *Carex*: 42.86%, average for all species: 26.36%). This indicates that *Carex* are disfavoured for all of the significant trait differences between the transferred hay and the reference sites. Earlier studies have shown that the majority of seeds in transferred hay are produced by a few species, which may neither be the species that are most abundant in the vegetation, nor the target species of the restoration (Klimkowska et al. 2009, 2010b). Our interpretation of the result is that the trait differences between the hay, and the reference sites it was harvested from, reflects that the majority of seeds in the hay are likely to come from ruderal and/or competitive species as opposed to typical *Carex* species of fens, which are stress tolerant species (high SLA species are rarely stress tolerators) that are adapted to the typical fen conditions of flooding and anoxia by i.e. development of aerenchyma (Fagerstedt 1992; Moog 1998).

This discrepancy between traits present in the hay samples and the traits presents in the reference sites the hay was taken from, is evident in the 79% lower functional richness (FRic) (74% lower when averaged over years 2 and 3) in the hay samples than in the reference sites, which shows that a large part of the potential trait diversity is filtered out in the process of hay harvesting.

Functional analysis of the major treatments

The significantly higher EMV in the restoration sites and reference sites compared to the control sites shows that species establishment along a moisture gradient in early stages of community assembly on bare peat largely follows behaviour of adult plants in established plant communities, for which Ellenberg values were established (Ellenberg et al. 1992).

The higher dominance of clonal lateral spread (CLS)-capacity and hydrochory among plants in the restoration sites compared to the control sites is most likely connected to differences in wetness between the sites, as both CLS-capacity and hydrochory are adaptations to waterlogged habitats (Soukupová 1994; Van den Broek et al. 2005). This explanation is supported by the interaction between elevation in the restoration site and CLS-capacity and hydrochory, revealed by the linear mixed effect model.

The much higher presence of anemochory in the control site compared to the restoration sites and reference sites is in line with earlier studies that have reported the lesser importance of anemochory compared to hydrochory for dispersal in freshwater wetlands (van Diggelen et al. 2006). Indeed, we do see the opposite results for hydrochory, which is expected due to the wetter conditions in the restoration sites and the reference sites.

Boars visited plots in the restoration sites to some degree, but caused large disturbance in the control sites. A total of ten control plots (five with hay dispersal and five without hay dispersal) were completely destroyed by boars between year 2 and 3. Our interpretation of the higher degree of animal dispersed plants in the control sites, is that it is influenced by the boars at the site.

The FD-analysis of the major treatments shows that the reference sites have a much higher degree of autochory than the restoration sites and the control sites. Our interpretation is that the hay from the reference site, contained a lower degree of autochorous species than the reference site from where it was harvested. Among the 129 species present in any plot during any year, 24 species had the capacity for autochory, which includes 86% of the *Carex* species in our study. Combined with the result from the hay sample analysis that illustrates the failure of transferring autochorous species, we have a strong imprint of our failure to restore the fen *Carex* community despite the directed action in the second year.

The significantly lower functional evenness (FEve) in the control site, compared to the restoration sites indicates a much higher niche overlap and/or less evenly distributed abundance among species in the control sites. The significantly lower functional divergence (FDiv) and functional dispersion (FDis) in the control sites compared to the restoration sites gives support to the possibility that it is the abundance distribution component of FEve that differ, and not the functional distance component of FEve (Mason et al. 2005). This tells us that the vegetation of the control site is dominated by few species.

The higher FDis in the restoration sites and the reference sites compared to the control sites, shows that we have a higher trait variation in these sites compared to the control sites (Villéger et al. 2008). This is in line with previous results from Kotowski et al. (2010) that a combination of waterlogging and canopy disturbance increases functional diversity.

Competition vs. habitat filtering

Our finding of a strong response of SLA to elevation above groundwater level is contrary to earlier studies that have shown that species with high SLA perform better in flooded (Violle et al. 2011) and anoxic (Mommer et al. 2006) conditions than low SLA species do. The reason for this is probably that the higher nutrient concentration in degraded fens compared to areas with less mineralised peat (Klimkowska et al. 2010a) has predominance here, so that low SLA species do better at low elevation in this case, despite lower diffusion capacity of oxygen. It is surprising that this effect should be evident at small differences in elevation with a linear trend. The response of EMV to elevation above groundwater level shows that species in the newly created restoration sites follow a wetness gradient similar to that of developed communities, which is evidence of habitat filtering. This habitat filtering along the elevation gradient also has a strong effect on the presence of CLS-capacity and hydrochory, both which are adaptations to waterlogged habitats (Soukupová 1994; Van den Broek et al. 2005). This strong filtering of several functional traits leaves an imprint on the overall filtering with a reduced FRic and FDis with decreasing elevation. The only significant difference in trait characteristics between the plots in the restoration site that received hay compared to those that didn't receive hay, is a lower abundance of plants with CLS-capacity in the plots that received hay transfer.

To summarisze, our results point to a strong habitat filter within the restoration sites that at low elevation reduces trait diversity and selects for species with high EMV and low SLA that have the capacity for CLS and hydrochory, but lack the capacity for autochory. The result from the species specific response analysis to differences in elevation above the groundwater level clearly

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illustrates the very strong filtering effect of elevation on individual species. The results from the linear mixed effect model show that the same environmental filter (the elevation gradient) also has a significant effect on several important functional traits, as well as a significant effect on FRic and FDis. Despite the high filtering at low elevation the restoration sites and the reference sites have a higher FDis than the control sites. That is, within the top-soil removal sites FDis and FRic decrease as elevation decrease, indicating an increased habitat filter most likely caused by anoxia at lower elevation. In the much higher elevated control sites where no top-soil removal was conducted, the FDis is much lower compared to the restoration sites or the reference sites. This is most likely caused by the status of the heavily degraded fen conditions with excess nutrients, which in the absence of top-soil removal creates a strong dominance of a few species (i.e. large cover of *F. rubra* and *U. dioica*).This is also revealed in the lower FEve in the control sites, which is caused by strong dominance of a few eutrophic species who can dominate efficiently in the absence of ground disturbance and anoxia. The highest functional diversity in fen restoration is thus achieved when competition is reduced (in this case by removal of excess nutrient, standing vegetation and an unwanted seed bank) and the habitat filter is increased (in this case by restoring the hydrology and its associated anoxic condition).

The value of a functional analysis to ecological restoration

A strong habitat filter should limit the spectrum of trait values that allow species to pass the filter and establish (Grime 1979; Huston 1979). This makes functional richness and functional dispersion good tools for detecting the presence of habitat filters. With functional evenness and functional divergence being measurements of resource utilisation and abundance distribution in a niche space respectively (Mason et al. 2005), they are good indicators of niche coverage and competition, where high competition leads to an increase in functional divergence. In our study we see the effect of the elevation gradient causing a strong filter that severely limits which species can establish, and at lower elevation we have a high dominance of a few species. An analysis of community weighted mean enabled us to draw conclusions about the response of individual traits to changes in environmental filters. By knowing which filters act in a particular restoration situation we may be able to foresee which types of species can be successfully introduced. In our opinion, the use of a functional diversity analysis in ecological restoration can provide managers with information regarding which environmental filters may influence the restoration outcome, and how this effect can be enhanced or diminished.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jnc.2013.08.004.

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Supplementary file

Functional diversity analysis helps to identify filters affecting community assembly after fen restoration by top-soil removal and hay-transfer

Running title: Identifying filters affecting community assembly

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1:1 Species-trait table

Functional traits for species present during any of the monitoring periods Year 1 (2009), Year 2 (2010) and Year 3 (2011). DM=Donor Meadow, TS=Top-soil removal site, CTRL=Control-site, SLA=Specific Leaf Area, CH=Canopy height, EMV=Ellenberg Moisture Value, CLS=Clonal Lateral Spread, Ane= Anemochory, AH=Animal-Human assisted dispersal, HC= Hydrochory, AC= Autochory, ×=present

Species	DM	TS	CTRL	SLA (mm^2/mg)	CH (m)	EMV	CLS	Ane	AH	HC	AC
Achillea millefolium	×	×	×	19.63	0.8	5	1	1	1	0	0
Agrostis canina		×		29.42	0.45	7	0	1	1	0	0
Agrostis stolonifera		×		32.58	0.4	6	1	1	1	0	0
Alisma plantago-aquatica		×		29.41	0.5	10	0	0	1	1	0
Alnus incana	×	×		28.14	25	7	1	1	0	0	0
Alopecurus pratensis		×		26.54	0.7	5	0	1	1	0	0
Anthoxanthum odoratum	×	×	×	28.41	0.25	6	0	1	1	0	0
Arabidopsis thaliana			×	33.81	0.5	3	0	1	0	0	0
Artemisia absinthium		×		24.8	1.1	4	0	1	1	0	0
Artemisia vulgaris		×		22.16	2.25	4	0	1	1	0	0
Betula pubescens	×	×		13.3	30	7	0	1	0	0	0
Bidens cernua		×	×	35.2	0.9	9	0	0	1	0	0
Bidens tripartite		×	×	32.5	0.9	8	0	0	1	0	0
Bistorta officinalis			×	32.4	0.8	7	0	1	1	0	0
Briza media	×			22.15	0.25	5	0	1	1	0	0
Bromus inermis	×			24.2	0.7	4	0	1	1	0	0
Calamagrostis canescens		×		24.51	1.3	9	0	1	1	0	0
Calamagrostis stricta	×			18.76	0.9	9	0	1	1	0	0
Caltha palustris	×			24.41	0.3	9	0	0	0	1	0
Cardamine pratensis		×		19.94	0.4	6	1	1	1	0	1

Cardaminopsis arenosa		×	×	28.57	0.2	4	0	1	0	0	0
Carex acuta	×		×	13.69	1.2	9	1	1	1	0	1
Carex hirta		×		19.79	0.8	7	1	1	1	1	1
Carex nigra	×		×	17.09	0.25	8	0	1	1	0	1
Carex ovalis	×			22.36	0.4	7	0	1	1	0	1
Carex pseudocyperus		×		22.73	0.5	9	0	1	1	1	1
Carex rostrata	×	×		15.86	0.7	10	0	1	1	1	1
Carex vesicaria		×		14.7	0.8	10	1	0	0	0	0
Cerastium holosteoides		×	×	25.83	0.32	5	0	1	0	1	0
Chenopodium album			×	17.99	1.4	5	0	1	0	1	0
Cicuta virosa		×		21.69	1.5	10	1	1	1	1	0
Cirsium arvense	×	×	×	14.68	1.5	6	1	1	1	0	0
Cirsium palustre	×	×	×	18.93	1.3	8	0	1	1	0	0
Conyza canadensis		×		22.24	0.9	4	0	1	1	0	0
Cyperus flavescens		×		34.21	0.3	7	0	1	1	0	0
Dactylis glomerata		×		23.95	1.1	5	1	1	1	0	0
Dactylorhiza incarnata	×	×		21.52	0.7	9	0	1	0	0	0
Deschampsia cespitosa	×	×	×	16.54	2	6	0	1	1	0	0
Echinochloa crus galli		×		27.76	0.85	5	0	0	1	0	0
Eleocharis palustris		×		10.31	1	10	1	1	1	0	0
Elymus caninus		×		27.85	0.9	6	0	1	1	0	0
Epilobium hirsutum		×	×	26.7	1.5	8	1	1	0	0	0
Epilobium montanum		×	×	26.72	0.8	6	1	1	0	0	0
Epilobium palustre	×	×	×	30.43	0.6	8	0	0	0	1	1
Epilobium parviflorum	×	×	×	28.88	0.8	9	0	1	0	0	0
Equisetum fluviatile	×	×	×	9.45	1.5	10	1	1	0	1	1
Equisetum pratense		×	×	10.24	0.5	7	1	1	0	0	1
Erigeron acris			×	19.33	0.55	5	0	1	1	0	0

Eriophorum angustifolium	×			7.28	0.57	9	1	1	0	0	0
Eupatorium cannabinum		×	×	27.39	1.5	8	0	1	1	0	0
Fallopia convolvulus			×	21.38	2	4	0	0	1	0	0
Festuca pratensis	×		×	24.6	0.8	6	0	1	1	0	0
Festuca rubra	×	×	×	20.99	0.9	5	0	1	1	0	0
Filipendula ulmaria			×	25.16	1.3	8	0	1	0	1	0
Frangula alnus	×			16.65	7	8	0	0	1	0	0
Galeopsis tetrahit			×	32.31	0.7	5	0	0	1	0	0
Galium palustre	×	×		36.46	1.2	9	0	1	1	0	0
Galium uliginosum	×	×	×	28.53	0.6	9	0	1	1	0	0
Galium verum		×		21.2	1	4	0	1	1	0	0
Geum rivale	×	×	×	22.3	0.6	7	0	0	1	0	0
Glyceria maxima			×	21.3	1.8	10	1	0	1	1	0
Helictotrichon pubescens	×		×	19.26	1.1	4	0	1	1	0	0
Heracleum sphondylium			×	23.44	2	5	0	1	1	0	0
Hieracium pilosella		×		16.7	0.1	4	1	1	1	0	0
Holcus lanatus	×	×	×	35.95	0.5	6	0	1	1	0	0
Hypericum maculatum	×	×	×	28.11	1	6	1	0	0	1	0
Juncus articulatus	×	×		24.98	0.45	9	1	1	1	0	0
Juncus conglomeratus	×	×		4.9	1	7	0	1	1	0	0
Juncus effusus	×	×		14.16	1.5	7	0	1	1	0	0
Leersia oryzoides		×		NA	0.8	9	1	1	1	0	0
Lemna minor		×		18.7	0.01	11	1	0	1	1	0
Lemna trisulca		×		19	0.01	12	1	0	1	1	0
Linaria vulgaris			×	19.21	0.8	4	1	1	0	0	1
Lotus corniculatus		×		20.62	1.7	4	1	0	0	0	1
Lotus pedunculatus	×	×	×	25.11	0.6	8	0	0	0	0	1
Lychnis flos-cuculi	×	×	×	24.17	0.75	9	0	1	0	0	0

Lycopus europeaus	×	×	×	63.35	1.3	8	1	0	0	0	1
Lysimachia thyrsiflora	×			38.09	0.7	10	0	0	0	0	1
Lythrum salicaria	×	×	×	41.8	1.2	9	1	0	1	0	0
Mentha aquatica	×	×		25.48	0.9	8	1	0	0	1	0
Mentha arvensis			×	35.03	0.6	7	0	0	0	1	0
Menyanthes trifoliata	×			25.25	0.3	10	0	1	0	1	0
Milum effusum		×		33.35	0.8	5	0	1	1	0	0
Myosotis arvensis	×	×		26.89	0.6	5	0	0	1	0	0
Myosotis scorpioides	×	×		38.8	0.7	9	0	0	0	1	0
Persicaria amphibia			×	17.03	0.75	10	1	0	0	1	0
Persicaria hydropiper		×	×	41.07	0.75	7	0	1	1	1	0
Phleum pratense			×	24.87	0.9	5	0	1	1	0	0
Plantago lanceolata	×	×	×	18.48	0.4	5	0	1	1	0	0
Plantago major		×		20.93	0.6	5	0	1	1	0	0
Poa annua	×		×	39.59	0.15	5	0	1	1	0	0
Poa palustris	×		×	22.8	1.1	9	0	1	1	0	0
Poa pratensis	×	×	×	22.39	0.5	5	0	1	1	0	0
Poa trivialis	×	×	×	31.71	0.4	6	0	1	1	0	0
Potentilla anserina	×	×	×	23.66	0.5	7	1	1	1	0	0
Potentilla palustris	×	×		19	0.9	9	1	0	0	1	0
Prunella vulgaris	×			33.85	0.3	5	0	0	1	0	1
Ranunculus acris	×	×	×	21.97	1	6	0	1	1	0	1
Ranunculus flammula		×	×	16.58	0.5	9	1	1	1	0	0
Ranunculus lingua	×	×		13.35	1.5	10	1	0	0	1	0
Ranunculus repens	×	×	×	25.53	0.6	7	1	0	0	0	1
Ranunculus sceleratus		×	×	33	0.6	8	0	0	0	1	0
Rhinanthus serotinus		×		20.24	0.7	6	0	1	1	1	0
Roegneria canina				27.85	0.9	6	0	1	1	0	0

Rorippa sylvestris		×		39.95	0.5	8	0	0	1	1	1
Rumex acetosa		×	×	32.19	1	5	0	1	1	1	0
Rumex crispus	×	×	×	26.21	1.5	6	1	1	1	1	0
Rumex maritimus		×		23.44	1	9	0	1	1	1	0
Sagina nodosa		×	×	11.44	0.15	7	0	1	0	0	0
Sagina procumbens			×	19.25	0.2	6	0	1	0	0	0
Salix alba		×		12.57	30	7	0	1	0	0	0
Salix cinerea	×	×	×	10.11	4	8	0	1	0	0	0
Salix glabra		×		NA	1	8	0	1	0	0	0
Salix purpurea		×		9.5	5	9	0	1	0	0	0
Salix repens		×		18.97	1.5	7	0	1	0	0	0
Scirpus sylvaticus	×			24.81	0.95	8	1	1	1	0	0
Sisymbrium irio		×		NA	0.6	3	0	1	0	0	1
Spirodela polyrhiza		×		29.81	0.01	11	1	0	1	1	0
Stellaria palustris	×	×	×	23.02	0.6	8	0	1	0	0	0
Symphytum officinale		×		22.82	1.2	7	0	0	1	0	0
Tanacetum vulgare		×		20.49	1.1	6	0	1	1	0	0
Trifolium hybridum		×		24.3	0.51	5	0	1	1	0	0
Trifolium repens		×	×	31.51	0.5	5	1	1	1	0	0
Typha latifolia		×		14.5	2	10	1	1	0	0	0
Urtica dioica		×	×	27.09	1.8	6	1	1	0	0	0
Valeriana officinalis	×		×	38.1	0.75	8	0	1	0	0	0
Veronica anagallis-aquatica		×		33.2	0.75	10	0	1	1	1	1
Veronica beccabunga		×		25.12	0.6	10	1	1	1	1	1
Veronica chamaedrys			×	29.07	0.4	5	0	1	1	1	1
Veronica scutellata		×		26.44	0.45	9	0	1	1	1	1

1:2 Criterions used in Leda

SLA
Leaf rehydration prioritized. If not available No leaf rehydration or Unknown. Values from Leaf hydration and No Leaf hydration were never mixed. Weighted averages with sample size as weight used when several values were present.

Canopy height:
Max value used. Largest value used when several values existed.

1:3 Species richness

Average species richness in the different restoration treatments. TS= Top-soil removal, SE=Standard Error, NA=Not Available

	Species nr					
	Year 1		Year 2		Year 3	
Treatment	Mean	SE	Mean	SE	Mean	SE
TS & hay	11.65	1.29	13.80	1.41	14.26	0.93
TS & no hay	10.15	1.19	10.85	1.34	13.50	1.09
No TS & hay	10.20	0.66	9.80	1.28	12.40	0.93
No TS & no hay	NA	NA	9.60	0.68	10.20	2.01
Reference-sites	NA	NA	15.60	1.33	16.00	1.32

The effect of abiotic/biotic parameters and time on Functional Diversity indices and Community Weighted Mean (CWM) of functional traits (num DF=numerator degrees of freedom, den DF=denominator degrees of freedom). FRic=Functional Richness, FEve=Functional Evenness, FDiv=Functional Divergence, FDis=Functional Dispersion, SLA=Specific Leaf Area, EMV=Ellenberg Moisture Value, CLS=Clonal Lateral Spread, CH=Canopy height and AH-dispersal=Animal Human assisted dispersal.

1:4 Table 1 a

The response of functional traits to major treatments for Year 1 (2009), Year 2 (2010) and Year 3 (2011). P=p-value from Wilcoxon 2-sample test (Wx). W=Wilcoxon W-statistics. CWM= Community Weighted Mean, SLA= Specific Leaf Area, CH= Canopy height, EMV= Ellenberg Moisture Values, CLS= Clonal Lateral Spread, Ane= Anemochory, AH-dispersal= Animal-Human assisted dispersal, HC=Hydrochory, AC=Autochory, FRic= Functional Richness, FEve= Functional Evenness, FDiv=Functional Divergence, FDis= Functional Dispersion.

		Year 1		Year 2		Year 3	
		p	W	p	W	p	W
CWM SLA	TS x CTRL	0.14	138	3.20E-05	146	0.10	121
	TS x DM			0.51	172	0.11	247
	DM x CTRL			2.32E-03	167	0.02	80
CWM CH	TS x CTRL	0.44	167	0.09	291	0.07	254
	TS x DM			0.48	229.5	0.81	195
	DM x CTRL			0.11	137	0.06	25
CWM EMV	TS x CTRL	1.36E-09	397	4.77E-16	800	1.16E-08	364
	TS x DM			1.53E-03	326	0.32	224
	DM x CTRL			4.66E-07	3	1.08E-05	0
CWM CLS	TS x CTRL	3.80E-04	347	2.42E-06	701	1.04E-07	358
	TS x DM			2.82E-05	373	0.01	288
	DM x CTRL			0.78	107	0.01	18
CWM Ane	TS x CTRL	5.66E-05	33.5	4.50E-06	107	2.38E-06	3
	TS x DM			0.74	214	0.59	164
	DM x CTRL			2.05E-04	179	1.82E-04	100
CWM AH-dispersal	TS x CTRL	0.12	136	0.40	345	5.38E-06	28
	TS x DM			0.73	185	0.93	181
	DM x CTRL			0.71	109	1.05E-03	91
CWM HC	TS x CTRL	0.01	308	2.38E-05	670	4.24E-05	343
	TS x DM			0.63	220.5	0.59	163.5
	DM x CTRL			0.02	45	3.25E-04	6
CWM AC	TS x CTRL	0.04	286.5	0.02	548	0.20	235
	TS x DM			8.48E-06	16	2.59E-08	8
	DM x CTRL			1.33E-07	1	1.08E-05	0
FRic	TS x CTRL	0.60	178	0.91	408	0.06	257
	TS x DM			0.21	148	0.10	122
	DM x CTRL			0.33	77	0.03	21
FEve	TS x CTRL	0.01	303	0.10	507	1.18E-03	30

	TS x DM			0.02	107	0.07	115
	DM x CTRL			1.35E-03	30	0.01	14
FDiv	**TS x CTRL**	0.86	208	0.35	340	1.46E-03	303
	TS x DM			0.68	182	0.10	249
	DM x CTRL			1.00	100	0.17	31
FDis	**TS x CTRL**	0.02	294	0.18	486	1.65E-05	336
	TS x DM			0.01	99	0.32	146
	DM x CTRL			0.01	42	3.25E-04	6

1:5: Table 1 b

Mean and SE values for functional traits of major treatments for Year 1 (2009), Year 2 (2010) and Year 3 (2011). TS= Top-soil removal site, CTRL= Control-sites, DM= Donor meadows (reference-sites), CWM= Community Weighted Mean, SLA= Specific Leaf Area, CH= Canopy height, EMV= Ellenberg Moisture Values, CLS= Clonal Lateral Spread, Ane= Anemochory, AH-dispersal= Animal-Human assisted dispersal, HC=Hydrochory, AC=Autochory, FRic= Functional Richness, FEve= Functional Evenness, FDiv=Functional Divergence, FDis= Functional Dispersion.

		TS			CTRL			DM	
		Year 1	Year 2	Year 3	Year 1	Year 2	Year 3	Year 2	Year 3
FRic	Mean	0.52	0.50	0.53	0.58	0.51	0.39	0.61	0.62
	SE	0.03	0.04	0.02	0.06	0.04	0.07	0.06	0.04
FEve	Mean	0.69	0.62	0.62	0.57	0.57	0.49	0.70	0.66
	SE	0.02	0.02	0.01	0.04	0.03	0.04	0.02	0.05
FDiv	Mean	0.83	0.77	0.89	0.84	0.80	0.77	0.80	0.82
	SE	0.02	0.02	0.01	0.03	0.03	0.03	0.03	0.03
FDis	Mean	0.14	0.14	0.15	0.10	0.11	0.08	0.17	0.16
	SE	0.01	0.01	0.01	0.02	0.01	0.01	0.01	0.01
CWM SLA	Mean	23.24	21.49	22.37	25.46	25.56	23.91	21.87	20.26
	SE	0.56	0.56	0.53	1.10	0.67	0.57	0.76	1.12
CWM CH	Mean	0.96	0.91	1.05	0.96	1.09	0.83	0.85	0.98
	SE	0.11	0.04	0.06	0.09	0.09	0.04	0.07	0.06
CWM EMV	Mean	8.55	9.18	8.91	5.88	6.09	6.04	8.07	8.65
	SE	0.18	0.16	0.18	0.19	0.13	0.22	0.23	0.19
CWM LS	Mean	0.70	0.77	0.70	0.28	0.35	0.11	0.28	0.43
	SE	0.04	0.04	0.04	0.09	0.06	0.04	0.04	0.09
CWM Ane	Mean	0.71	0.69	0.68	0.96	0.90	0.97	0.66	0.72
	SE	0.04	0.03	0.03	0.01	0.02	0.01	0.05	0.05
CWM AH-dispersal	Mean	0.67	0.61	0.61	0.77	0.65	0.87	0.64	0.60
	SE	0.03	0.03	0.03	0.07	0.06	0.04	0.05	0.08
CWM HC	Mean	0.30	0.28	0.25	0.12	0.07	0.03	0.24	0.32
	SE	0.04	0.04	0.03	0.05	0.02	0.01	0.06	0.09
CWM AC	Mean	0.11	0.12	0.16	0.04	0.05	0.09	0.49	0.61
	SE	0.02	0.02	0.02	0.01	0.01	0.02	0.05	0.06

1:6: Table 2

A comparison of the functional-trait characteristics of the seeds in harvested hay from the donor meadows and the standing vegetation in the donor meadows for Year 2 (2010) – Year 3 (2011) made from abundance (Ab) data and presence/absence-data (P/A). DM= Donor meadow vegetation from where the hay was mown and collected, Hay= Hay samples of the mown and collected hay from the donor-meadows (reference-sites) P=p-value from Wilcoxon 2-sample test (Wx). W=Wilcoxon W-statistics, SE= Standard Error, CWM= Community Weighted Mean, SLA= Specific Leaf Area, CH= Canopy height, EMV= Ellenberg Moisture Values, CLS= Clonal Lateral Spread, Ane= Anemochory, AH-dispersal= Animal-Human assisted dispersal, HC=Hydrochory, AC=Autochory, FRic= Functional Richness, FEve= Functional Evenness, FDiv=Functional Divergence, FDis= Functional Dispersion.

		DM Year 2 x Hay				DM Year 3 x Hay				Hay	
Method	**Index**	**P**	**w**	**Mean**	**SE**	**p**	**w**	**Mean**	**SE**	**Mean**	**SE**
Ab	**FRic**	0.01	126	4.66E-04	1.49E-04	4.28E-04	143	5.38E-04	1.15E-04	1.15E-04	1.90E-05
	FEve	0.14	109	0.87	0.01	0.17	107	0.88	0.01	0.85	0.01
	FDiv	0.24	57	0.80	0.02	0.62	90	0.84	0.02	0.83	0.02
	FDis	0.70	88	0.19	0.01	0.18	106	0.20	0.01	0.18	0.01
	CWM SLA	4.52E-06	4	23.42	0.56	4.52E-06	4	22.64	0.89	28.59	0.61
	CWM CH	0.62	90	1.01	0.12	0.15	108	0.99	0.08	0.86	0.01
	CWM EMV	3.04E-04	149	7.85	0.20	2.77E-05	160	8.28	0.18	6.64	0.14
	CWM CLS	0.12	50	0.28	0.03	0.51	93	0.37	0.04	0.35	0.02
	CWM Ane	0.77	74	0.68	0.02	0.21	55.5	0.63	0.02	0.74	0.05
	CWM AH-dispersal	0.43	95.5	0.64	0.03	0.85	76	0.56	0.05	0.56	0.05
	CWM HC	0.04	119.5	0.19	0.04	1.30E-04	153	0.27	0.05	0.09	0.01
	CWM AC	2.44E-03	138	0.37	0.02	1.07E-04	154	0.45	0.03	0.23	0.02
P/A	**FRic**	0.01	126	4.66E-04	1.49E-04	4.28E-04	143	5.38E-04	1.15E-04	1.15E-04	1.90E-05
	FEve	0.82	75	0.97	2.08E-03	0.66	89	0.97	2.29E-03	0.97	1.17E-03
	FDiv	0.01	28	0.79	0.01	0.70	72	0.83	0.01	0.84	0.01
	FDis	0.74	87	0.19	0.01	0.06	116	0.20	3.55E-03	0.19	4.28E-03
	CWM SLA	2.64E-06	3	24.47	0.35	2.52E-05	8	23.56	0.87	28.71	0.59

CWM CH	0.06	116	1.17	0.22	0.01	130	1.04	0.13	0.82	0.02
CWM EMV	1.32E-04	153	7.72	0.18	3.49E-05	159	8.13	0.18	6.60	0.10
CWM CLS	0.04	40.5	0.28	0.02	0.96	81.5	0.35	0.03	0.34	0.02
CWM Ane	0.09	47.5	0.69	0.02	0.02	35.5	0.65	0.02	0.77	0.03
CWM AH-dispersal	0.28	101	0.63	0.03	0.83	84.5	0.57	0.05	0.56	0.04
CWM HC	0.04	118.5	0.17	0.03	1.57E-04	152	0.25	0.04	0.09	0.02
CWM AC	0.01	131.5	0.31	0.02	2.00E-04	151	0.38	0.02	0.23	0.01

1:7 Table 3

The effect of abiotic/biotic parameters on Functional Diversity indices and Community Weighted Mean (CWM) of functional traits. Bonferroni correction applied with the significance level set to α/n_y (α =0.05, n_y=12). El = Elevation, Yr = Year, num DF= numerator degrees of freedom, Tr= Transformation, den DF= denominator degrees of freedom, minus sign=no transformation, sqrt= square root, FRic= Functional Richness, FEve=Functional Evenness, FDiv= Functional Divergence, FDis= Functional Dispersion, SLA= Specific Leaf Area, HC= Hydrochory, EMV= Ellenberg Moisture Value, CLS= Clonal Lateral Spread, CH=Canopy height, AC=Autochory, AH= Animal-Human assisted dispersal, Ane= Anemochory.

			FRic				FEve				FDiv		
Source	**num DF**	**Tr**	**den DF**	**F**	**p**	**Tr**	**den DF**	**F**	**p**	**Tr**	**den DF**	**F**	**p**
El	1	–	33	14.87	5.00E-04	–	30	0.18	0.68	–	30	3.99	0.05
Hay	1	–	33	2.24	0.14	–	30	10	3.60E-03	–	30	3.11	0.09
Hay x El	1	–	33	0.14	0.71	–	30	12.27	1.50E-03	–	30	0.07	0.8
Yr	2	–	64	0.06	0.94	–	58	5.57	0.01	–	58	11.72	1.00E-04
Yr x El	2	–	64	4.3	0.02	–	58	3.09	0.05	–	58	1.64	0.2
Yr x Hay	2	–	64	0.36	0.7	–	58	2.25	0.11	–	58	11.34	1.00E-04
Yr x Hay x El	2	–	64	0.44	0.64	–	58	3.26	0.05	–	58	3.32	0.04
			FDis				**SLA**				**HC**		
Source	**num DF**	**Tr**	**den DF**	**F**	**p**	**Tr**	**den DF**	**F**	**p**	**Tr**	**den DF**	**F**	**p**
El	1	–	33	12.87	1.10E-03	–	33	14.49	6.00E-04	sqrt	33	41.43	<0.0001
Hay	1	–	33	6	0.02	–	33	3.52	0.07	sqrt	33	1.8	0.19
Hay x El	1	–	33	3.6	0.07	–	33	0.23	0.64	sqrt	33	0	1
Yr	2	–	64	1.29	0.28	–	64	4.98	0.01	sqrt	64	0.65	0.53
Yr x El	2	–	64	0.15	0.86	–	64	1.47	0.24	sqrt	64	5.38	0.01
Yr x Hay	2	–	64	2.09	0.13	–	64	0.84	0.44	sqrt	64	0.04	0.96
Yr x Hay x El	2	–	64	0.97	0.39	–	64	2.63	0.08	sqrt	64	0.16	0.85
			EMV				**CLS**				**CH**		
Source	**num DF**	**Tr**	**den DF**	**F**	**p**	**Tr**	**den DF**	**F**	**p**	**Tr**	**den DF**	**F**	**p**
El	1	–	33	49.16	<0.0001	–	33	112.9	<0.0001	$\log_{10}$(CH+1)	30	3.16	0.09

Hay	1	–	33	6.83	0.01	–	33	18.05	2.00E-04	$\log_{10}$(CH+1)	30	3.5	0.07
Hay x El	1	–	33	0.18	0.67	–	33	3.32	0.08	$\log_{10}$(CH+1)	30	7.09	0.01
Yr	2	–	64	11.98	<0.0001	–	64	6.22	3.40E-03	$\log_{10}$(CH+1)	58	5.33	0.01
Yr x El	2	–	64	0.61	0.55	–	64	1.3	0.28	$\log_{10}$(CH+1)	58	1.33	0.27
Yr x Hay	2	–	64	0.36	0.7	–	64	3.33	0.04	$\log_{10}$(CH+1)	58	0.09	0.91
Yr x Hay x El	2	–	64	0.32	0.73	–	64	1.17	0.32	$\log_{10}$(CH+1)	58	0.47	0.63
				AC				**AH**				**Ane**	
Source	**num DF**	**Tr**	**den DF**	**F**	**p**	**Tr**	**den DF**	**F**	**p**	**Tr**	**den DF**	**F**	**p**
El	1	sqrt	33	17.93	2.00E-04	–	32	0.29	0.6	–	33	7.56	0.01
Hay	1	sqrt	33	3.17	0.08	–	32	0.35	0.56	–	33	0.02	0.88
Hay x El	1	sqrt	33	4.37	0.04	–	32	1.03	0.32	–	33	0.33	0.57
Yr	2	sqrt	64	3.55	0.03	–	62	1.68	0.19	–	64	0.23	0.79
Yr x El	2	sqrt	64	1.99	0.15	–	62	0.5	0.61	–	64	1.43	0.25
Yr x Hay	2	sqrt	64	0.03	0.97	–	62	0.06	0.94	–	64	0.94	0.4
Yr x Hay x El	2	sqrt	64	0.02	0.98	–	62	1.92	0.16	–	64	1.58	0.21

Declarations of authors

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2013-11-04

DECLARATION

I declare that in the publication *"New nature by sowing? The current state of species introduction in grassland restoration, and the road ahead"*, Petter Hedberg, Wiktor Kotowski (*Journal for Nature Conservation*, Volume 18, Issue 4, December 2010, Pages 304-308, ISSN: 1617-1381, DOI: 10.1016/j.jnc.2010.01.003), my contribution concerned searching and analysing case studies, writing the manuscript, accounting for co-authors´ comments and accounting for reviewers' comments.

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I declare that in the publication *"Vegetation recovery after multiple-site experimental fen restorations"*, Petter Hedberg, Wiktor Kotowski, Peter Saetre, Kalle Mälson, Håkan Rydin, Sebastian Sundberg (*Biological Conservation*, Volume 147, Issue 1, March 2012, Pages 60-67, ISSN: 0006-3207, DOI: 10.1016/j.biocon.2012.01.039), my contribution concerned monitoring, analysing data, writing manuscript, accounting for comments of co-authors´ comments and accounting for reviewers´ comments.

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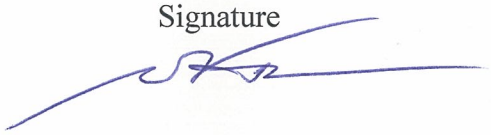

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I declare that in the publication *"A functional trait approach to fen restoration analysis"*, Petter Hedberg, Peter Saetre, Sebastian Sundberg, Håkan Rydin, Wiktor Kotowski (*Applied Vegetation Science,* 16, 2013, Pages 658-666, ISSN: 1654-109X, DOI: 10.1111/avsc.12042), my contribution concerned monitoring, compiling trait-data, statistical analysis, writing the manuscript, accounting for co-authors´ comments and accounting for reviewers´ comments.

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4 Nov 2013

DECLARATION

I declare that in the publication *"A functional trait approach to fen restoration analysis"*, by Petter Hedberg, Peter Saetre, Sebastian Sundberg, Håkan Rydin, Wiktor Kotowski (*Applied Vegetation Science,* 16, 2013, Pages 658-666, ISSN: 1654-109X, DOI: 10.1111/avsc.12042), my contribution concerned assisting with monitoring during the first years and providing feedback to the first author´s manuscript.

Signature

Wiktor Kotowski

Department of Plant Ecology and Environmental Conservation

Faculty of Biology

University of Warsaw

2013-11-04

DECLARATION

I declare that in the publication *"A functional trait approach to fen restoration analysis"*, Petter Hedberg, Peter Saetre, Sebastian Sundberg, Håkan Rydin, Wiktor Kotowski, (*Applied Vegetation Science,* 16, 2013, Pages 658-666, ISSN: 1654-109X, DOI: 10.1111/avsc.12042), my contribution concerned idea of data analysis, assisting with monitoring and providing supervision to the first author of the manuscript.

Signature

Petter Hedberg

Department of Plant Ecology and Environmental Conservation

Faculty of Biology

University of Warsaw

2013-11-04

DECLARATION

I declare that in the publication " Functional diversity analysis helps to identify filters affecting community assembly after fen restoration by top-soil removal and hay-transfer", Petter Hedberg, Łukasz Kozub, Wiktor Kotowski (Journal for Nature Conservation, 2013 DOI: 10.1016/j.jnc.2013.08.004), my contribution concerned dispersal of hay, depth measurements, monitoring, compiling trait data, statistical analysis, writing of manuscript, accounting for comment of co-authors´ and accounting for comments from reviewers´.

Signature

Łukasz Kozub 2013-11-04

Department of Plant Ecology and Environmental Conservation

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DECLARATION

I declare that in the publication " Functional diversity analysis helps to identify filters affecting community assembly after fen restoration by top-soil removal and hay-transfer", Petter Hedberg, Łukasz Kozub, Wiktor Kotowski, Journal for Nature Conservation, 2013, DOI: 10.1016/j.jnc.2013.08.004, my contribution concerned assisting with dispersal of hay and assisting with depth measurements.

Signature

Wiktor Kotowski

Department of Plant Ecology and Environmental Conservation

Faculty of Biology

University of Warsaw

2013-11-04

DECLARATION

I declare that in the publication "Functional diversity analysis helps to identify filters affecting community assembly after fen restoration by top-soil removal and hay-transfer", Petter Hedberg, Łukasz Kozub, Wiktor Kotowski (Journal for Nature Conservation, 2013 DOI: 10.1016/j.jnc.2013.08.004), my contribution concerned idea of the project, securing funds for the restoration measures and the research grant, experimental design, assisting with dispersal of hay and species monitoring and supervising the first author of the manuscript.

Signature